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New Series, No. 3

A MONOGRAPH OF CLASMATOCOLEA (HEPATICAE)

JOHN J. ENGEL

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Publication 1311

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JOHN J. ENGEL
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Department of Botany
Field Museum of Natural History

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DONALD RICHARDS

TABLE OF CONTENTS

ACKNOWLEDGMENTS 1
I. HISTORY 3
II. SOME METHODS AND TERMINOLOGY 5
III. TAXONOMIC CHARACTERS AND MORPHOLOGY 7
Slime papillae 7
Branching 8
Stems 10
Endophytic hyphae 11
Rhizoids 11
Leaves 11
Leaf cells and oil-bodies 12
Underleaves 13
Androecia 13
Bracts 14
Bracteoles 15
Perianths 15
Setae 17
Capsules 17
Spores 18
Elaters 19
IV. COMPARATIVE MORPHOLOGICAL DIVERSITY AND EVOLUTION OF SPOROPHYTE AND GAMETOPHYTE 19
Artificial key to taxa based upon sporophyte material 20
V. ORIGIN OF CLASMATOCOLEA AND SOME EVOLUTIONARY TRENDS 21
VI. GENERIC RELATIONSHIPS OF CLASMATOCOLEA 24
VII. PHYTOGEOGRAPHY 29
VIII. CONSPECTUS OF TAXA 38
IX. CLASMATOCOLEA 39
X. KEY TO TAXA OF CLASMATOCOLEA 40
XI. EXCLUDENDA 190
REFERENCES 198
SCANNING ELECTRON MICROGRAPHS 204
INDEX OF TAXA 225

LIST OF ILLUSTRATIONS

Figures

1. Diagrammatic representation of suggested major evolutionary lines in *Clasmatocolea* 22
2. Pictorial representation of generic relationships in Lophocoleaceae 25
3. Reconstruction of continental blocs at the end of the Triassic (180 m. y. BP) 32
4. Reconstruction of Permian positions of Gondwanaland continents 33
5. Reconstruction of continental blocs at the end of the Jurassic (135 m. y. BP) 34
6. Reconstruction of continental blocs at the end of the Cretaceous (65 m. y. BP) 36
7. *Clasmatocolea rigens* (Hook. f. & Tayl.) Engel 45
8. *Clasmatocolea rigens* (Hook. f. & Tayl.) Engel 46
9. Map of *Clasmatocolea rigens* (Hook. f. & Tayl.) Engel 47
10. *Clasmatocolea obvoluta* (Hook. f. & Tayl.) Grolle 51
11. *Clasmatocolea obvoluta* (Hook. f. & Tayl.) Grolle 52
12. *Clasmatocolea obvoluta* (Hook. f. & Tayl.) Grolle 53
13. Map of *Clasmatocolea obvoluta* (Hook. f. & Tayl.) Grolle 54
14. *Clasmatocolea trachyopa* (Hook. f. & Tayl.) Grolle 61
15. *Clasmatocolea trachyopa* (Hook. f. & Tayl.) Grolle 62
16. *Clasmatocolea trachyopa* (Hook. f. & Tayl.) Grolle 63
17. Map of *Clasmatocolea trachyopa* (Hook. f. & Tayl.) Grolle 64
18. *Clasmatocolea marginata* (Steph.) Grolle 70
19. *Clasmatocolea marginata* (Steph.) Grolle 71
20. *Clasmatocolea marginata* (Steph.) Grolle 72
21. *Clasmatocolea humilis* (Hook. f. & Tayl.) Grolle 75
22. *Clasmatocolea humilis* (Hook. f. & Tayl.) Grolle 76
23. *Clasmatocolea humilis* (Hook. f. & Tayl.) Grolle 78
24. Map of *Clasmatocolea humilis* (Hook. f. & Tayl.) Grolle 79
25. *Clasmatocolea fasciculata* (Nees) Grolle 92
26. *Clasmatocolea fasciculata* (Nees) Grolle 93
27. Map of *Clasmatocolea fasciculata* (Nees) Grolle 94
28. *Clasmatocolea vermicularis* (Lehm.) Grolle 98
29. *Clasmatocolea vermicularis* (Lehm.) Grolle 100
30. Map of *Clasmatocolea vermicularis* (Lehm.) Grolle 106
31. *Clasmatocolea gayana* (Mont.) Grolle 113
32. *Clasmatocolea gayana* (Mont.) Grolle 114
33. Map of *Clasmatocolea gayana* (Mont.) Grolle 115
34. *Clasmatocolea ctenophylla* (Schiffn.) Grolle 120
35. Map of *Clasmatocolea ctenophylla* (Schiffn.) Grolle 122
36. *Clasmatocolea crassiretis* (Herz.) Grolle 125
37. Map of *Clasmatocolea crassiretis* (Herz.) Grolle 126

38. *Clasmatocolea moniliformis* Engel..... 129
39. Map of *Clasmatocolea moniliformis* Engel..... 130
40. *Clasmatocolea minutiretis* Engel & Grolle..... 134
41. *Clasmatocolea minutiretis* Engel & Grolle..... 135
42. Map of *Clasmatocolea minutiretis* Engel & Grolle 136
43. *Clasmatocolea fulvella* (Hook. f. & Tayl.) Grolle..... 140
44. *Clasmatocolea fulvella* (Hook. f. & Tayl.) Grolle..... 142
45. Map of *Clasmatocolea fulvella* (Hook. f. & Tayl.) Grolle..... 145
46. *Clasmatocolea strongylophylla* (Hook. f. & Tayl.) Grolle..... 148
47. Map of *Clasmatocolea strongylophylla* (Hook. f. & Tayl.) Grolle..... 152
48. *Clasmatocolea tjiwideiensis* (Sande-Lac.) Grolle..... 156
49. *Clasmatocolea puccioana* (De Not.) Grolle..... 158
50. *Clasmatocolea puccioana* (De Not.) Grolle..... 160
51. Map of *Clasmatocolea puccioana* (De Not.) Grolle..... 163
52. *Clasmatocolea navistipula* (Steph.) Grolle..... 166
53. *Clasmatocolea navistipula* (Steph.) Grolle..... 168
54. Map of *Clasmatocolea navistipula* (Steph.) Grolle..... 170
55. *Clasmatocolea notophylla* (Hook. f. & Tayl.) Grolle..... 174
56. Map of *Clasmatocolea notophylla* (Hook. f. & Tayl.) Grolle..... 175
57. *Clasmatocolea verrucosa* Engel..... 180
58. *Clasmatocolea verrucosa* Engel..... 181
59. *Clasmatocolea cucullistipula* (Steph.) Grolle..... 184
60. *Clasmatocolea cucullistipula* (Steph.) Grolle..... 185
61. Map of *Clasmatocolea cucullistipula* (Steph.) Grolle..... 188

Plates

1. *Clasmatocolea rigens* (Hook. f. & Tayl.) Engel. ×5,000..... 204
2. *Clasmatocolea rigens* (Hook. f. & Tayl.) Engel. ×10,000..... 205
3. *Clasmatocolea obvoluta* (Hook. f. & Tayl.) Grolle. ×4,700..... 206
4. *Clasmatocolea obvoluta* (Hook. f. & Tayl.) Grolle. ×9,500..... 206
5. *Clasmatocolea trachyopa* (Hook. f. & Tayl.) Grolle. ×5,000..... 207
6. *Clasmatocolea trachyopa* (Hook. f. & Tayl.) Grolle. ×10,000..... 207
7. *Clasmatocolea humilis* (Hook. f. & Tayl.) Grolle. ×6,600..... 208
8. *Clasmatocolea humilis* (Hook. f. & Tayl.) Grolle. ×9,700..... 209
9. *Clasmatocolea humilis* (Hook. f. & Tayl.) Grolle. ×28,600..... 210
10. *Clasmatocolea humilis* (Hook. f. & Tayl.) Grolle. ×46,000..... 211
11. *Clasmatocolea vermicularis* (Lehm.) Grolle. ×5,000..... 212
12. *Clasmatocolea vermicularis* (Lehm.) Grolle. ×10,000..... 212
13. *Clasmatocolea gayana* (Mont.) Grolle. ×3,655..... 213
14. *Clasmatocolea gayana* (Mont.) Grolle. ×10,260..... 214
15. *Clasmatocolea ctenophylla* (Schiffn.) Grolle. ×5,000..... 215
16. *Clasmatocolea ctenophylla* (Schiffn.) Grolle. ×10,000..... 215
17. *Clasmatocolea minutiretis* Engel & Grolle. ×5,400..... 216
18. *Clasmatocolea minutiretis* Engel & Grolle. ×10,750..... 216
19. *Clasmatocolea fulvella* (Hook. f. & Tayl.) Grolle. ×5,400..... 217
20. *Clasmatocolea fulvella* (Hook. f. & Tayl.) Grolle. ×10,750..... 218
21. *Clasmatocolea strongylophylla* (Hook. f. & Tayl.) Grolle. ×5,240..... 218
22. *Clasmatocolea strongylophylla* (Hook. f. & Tayl.) Grolle. ×10,000..... 219
23. *Clasmatocolea puccioana* (De Not.) Grolle. ×6,075..... 219
24. *Clasmatocolea puccioana* (De Not.) Grolle. ×12,100..... 220

25. *Clasmatocolea puccioana* (De Not.) Grolle. ×25,300..... 221
26. *Clasmatocolea navistipula* (Steph.) Grolle. ×5,000..... 222
27. *Clasmatocolea navistipula* (Steph.) Grolle. ×10,000..... 222
28. *Clasmatocolea cucullistipula* (Steph.) Grolle. ×3,100..... 223
29. *Clasmatocolea cucullistipula* (Steph.) Grolle. ×10,200..... 224

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I. HISTORY

The genus *Clasmatocolea* has been misunderstood for the majority of time since its inception. The confusion over the circumscription and taxonomic position of the genus persisted until the work of Grolle (1960).

Clasmatocolea was described by Spruce (1885) in his classic *Hepaticae Amazonicae et Andinae*. Spruce placed *Clasmatocolea* between *Lophocolea* and *Chiloscyphus* and stated (p. 440), "These curious little plants come very near Lophocolea. . . ." He included three species in *Clasmatocolea—C. cuneifolia*, *C. fragillima*, and *C. heterostipa*, the first was a transfer from *Jungermannia*, and the latter two were new.

Schiffner (1893), in his treatment of Hepaticae in Engler and Prantl's *Die Natürlichen Pflanzenfamilien*, placed *Clasmatocolea* between *Leioscyphus* and *Apothomanthus*, and then followed the latter with *Lophocolea*. Schiffner recognized the same three *Clasmatocolea* species as Spruce.

Stephani added *C. chilensis* in 1900. In his *Species Hepaticarum* (1906), he presented the following sequence of genera: *Leioscyphus-Southbya-Arnellia-Gongylanthus-Clasmatocolea-Lophocolea*. In the genus *Clasmatocolea*, Stephani included six species, and much of the subsequent confusion over the identity of *Clasmatocolea* can be traced to the particular species he included. Stephani transferred *Jungermannia doellingeri* Nees to *Clasmatocolea* and cited the species first in his generic treatment. Stephani's concept of *Clasmatocolea* included various taxa such as *C. exigua*, which he regarded as similar to *Jungermannia doellingeri*. Further, his version of *C. heterostipa* is doubtful, since according to Grolle (1956), a specimen of it is not represented in the Stephani Herbarium. Stephani included elements of several of these diverse species, including *Clasmatocolea* (= *Chonecolea*) *doellingeri*, in his generic diagnosis. Of the six species that Sephani included in *Species Hepaticarum*, four—*C. doellingeri*, *C. exigua*, *C. truncata*, and *C. fragillima*—were subsequently found to belong to other genera in four different families. As Grolle (1956, p. 288) points out, "Vielleicht hat Stephani die Spruce'schen Arten von *Clasmatocolea* nicht gut gekannt."

After Stephani treated *Clasmatocolea* in *Species Hepaticarum*, this genus was only incidentally dealt with during the next 50 years. Verdoorn (1932) included *Clasmatocolea* in the Epigonanthaceae, Evans (1939), in the Harpanthaceae, and Müller (1939-40), in the Plagiochilaceae. In 1943 Herzog transferred *Lophocolea flavovirens* Steph. to the genus, and in the same year Frye and Clark placed *Clasmatocolea* in the Lophocoleoideae, near *Chiloscyphus*. Frye and Clark included only *C. doellingeri* and *C. exigua* and published a generic diagnosis consisting of a mixture of *Clasmatocolea* sensu Spruce and *Chonecolea doellingeri*. Müller (1951-58) placed *Clasmatocolea* in the Plagiochilaceae, and Herzog & Noguchi (1955) published *C. innovata*. Until the 1950's, then, the genus was a heterogenous and quite misunderstood one, consisting of eight species, five of which were later shown to belong to as many different families.

Grolle (1956) revised the genus and regarded *Clasmatocolea* as having but one species, *C. heterostipa*, which he described in full and illustrated. At this time, Grolle thought *Clasmatocolea* was distinguishable by the two-layered capsule wall (differing from *Lophocolea*, which Grolle stated had a four- to five-stratose capsule wall) and the wide, entire perianth mouth. In this paper, Grolle excluded a number of species and described two new genera. He also considered relationships of *Clasmatocolea* to both Harpanthaceae and Lophocoleaceae, but refrained from a familial placement; at the same time he raised the question whether these two families were independent. Two years later Schuster (1958) placed *Clasmatocolea* in the Harpanthaceae.

Grolle (1959), in his treatment of African *Lophocolea*, did not recognize *Clasmatocolea*, but placed *C. heterostipa* in the synonymy of *Lophocolea subintegra*, thus giving it an amphiatlantic distribution.

In 1960, Grolle reelevated the genus to generic rank, excluded the features he earlier chose to differentiate the genus, and distinguished *Clasmatocolea* by concave leaves coupled with anatomy of the inner capsule wall layer. Grolle found the generitype, *C. heterostipa*, related not to *Lophocolea*, as he thought a year previously, but rather to numerous austral species, most of which were then called *Lophocolea*. For these reasons, Grolle (1960) transferred 18 species to *Clasmatocolea*. In this paper, he placed *Clasmatocolea* in the Lophocoleaceae, and Schuster concurred in 1966.

After 1960, seven more taxa were transferred to the genus by Grolle (1962, 1966, 1969, 1971, 1972b) and two by Engel (1973a). It is interesting to note that since 1900 *no* taxa had been described in *Clasmatocolea* (*s. str.*) until Engel (1979a and 1980).

Engel (1978) treated the Brunswick Peninsula taxa, therein reduced a number of species to synonymy for the first time, and presented a key to the species of that area.

Taxa (including varieties) here included in *Clasmatocolea* (*i.e.*, the genus in the strict sense) were described in a number of different genera. This wide array of genera underscores the degree of confusion that existed over the taxonomic position of these plants. Of the 20 names in *Jungermannia*, 14 later were transferred to *Lophocolea*, so that there existed a large pool of names under *Lophocolea*, with the remainder under a wide variety of miscellaneous genera. The basionyms are organized as follows:

Genus of basionym	*Number of taxa*	*Described mostly by*	*Range of publication*	*Percent of total*
Lophocolea	42	Stephani (25), Herzog (9), Schiffner (3), Massalongo (3)	1885-1958	50
Jungermannia	20	Hooker f. & Taylor (11), Lehmann (3), De Notaris (2)	1820-59	23.8
Clasmatocolea	7	Spruce, Stephani, Engel	1885-1980	8.3
Chiloscyphus	6	Various	1851-1915	7.1
Jamesoniella	1	Stephani	1911	1.2
Leioscyphus	1	Pearson	1922	1.2
Notoscyphus	1	Mitten	1877	1.2
Nardia	1	Stephani	1897	1.2
Alicularia	1	Herzog	1921	1.2
Conoscyphus	1	Pearson	1922	1.2
Blepharostoma	1	Gola	1923	1.2
Odontoschisma	1	Sim	1926	1.2
Isotachis	1	Stephani *ex* Herzog	1952	1.2
Total	84			

II. SOME METHODS AND TERMINOLOGY

All information pertaining to the vegetative plant parts, unless otherwise stated, was obtained from the main axis. The axis width was made by measuring the main axis, ventral side down, without altering the leaf direction, *i.e.*, without spreading the leaves. Axes that could not be balanced for such a view were maintained in that position by laterally bolstering them. Underleaf vs. stem width was obtained by dissecting underleaves, which were then flattened, measured, and compared to the stem width.

Leaf cell trigone size and terminology follows Schuster (1966).

A few reagents were used. Endophytic hyphae were stained with the use of cotton blue. Ammonium hydroxide was used as a clearing agent

for antheridia and setae when cells were obscured by enclosed foodstuffs.

For all American taxa, capsules from several different collections were selected, and their spores were prepared for scanning electron microscopy. Spore micrographs were made from several of these different capsules and later compared. Further, under the SEM, numerous spores were examined to determine if spore variation was present in that capsule. The spore micrographs, found on pages 204 to 224, represent those typical of the species. Spores, in some cases, were prepared using a standard Critical Point Drying technique. Micrographs were taken using a Cambridge Stereoscan S-4 microscope located at Field Museum.

Author citations follow the abbreviations in Sayre et al. (1964). Journals are abbreviated according to *Botanico-Periodicum-Huntianum* (B-P-H). Those authors and journals not in these references are abbreviated in a similar style. Herbarium citations follow *Index Herbariorum* (Holmgren & Keuken, 1974).

The terms Magellanian and Valdivian are frequently found in phytogeographical statements of species. These terms are defined in the section on phytogeography (pp. 29–30). The expression Patagonian Channels, however, is not defined elsewhere. I have used this term to indicate the highly dissected portion of western Chile south of Puerto Montt to and including the Brunswick Peninsula (*i.e.*, latitudes 41° 28′ S. to 53° 30′ S.). It includes the western portion of the mainland and the channels near Puerto Natales, S. Skyring, S. Otway, etc.

The terms West Patagonia and Andean Patagonia are used according to the following definitions given by Skottsberg (1910, 1916) and Moore (1968): *West Patagonia*—The region including the west slope of the Andes to the Pacific Ocean, characterized by high precipitation and supportive of lush rain forests and magellanian moorland. *Andean Patagonia*—The eastern slope of the Andes from base to snowline. This region experiences moderate rainfall and supports a deciduous, comparatively dry forest. Hueck (1966) recognizes two forested regions that extend to Andean Patagonia, the Northern *Nothofagus* forests, which are composed predominantly of two species of deciduous *Nothofagus*, *N. obliqua* and *N. procera*, and the *Araucaria-Libocedrus* zone.

The localities are cited in the manner provided in the following gazetteers: South Africa (Leistner & Morris, 1976); New Zealand (New Zealand Dept. of Lands and Survey, 1968, and U.S. Board on Geographic Names, 1954); and Peru, Australia, Brazil, Colombia, Chile, Argentina (U.S. Office of Geography, 1955, 1957, 1963, 1964, 1967, 1968, respectively).

Abbreviations of localities follow the American Geographical Society

index to map of Hispanic America (see American Geographical Society of New York. Index . . . , 1945, pp. 10-11) and are as follows:

A.—Arroyo
B.—Bahía, Bay
Bo.—Boca
Br.—Brazo
Cta.—Caleta
Can.—Canal
C.—Cerro
Cord.—Cordillera
Cr.—Creek
Ens.—Ensenada
Esto.—Estero, Estuario
F.—Fiordo
Fo.—Fondeadero
G.—Gulf
Hr.—Harbor
I.—Île, Isla, Island
L.—Lago, Lake
La.—Laguna
M.—Monte
Mt.—Mount, Mountain
P.—Peak
Pen.—Peninsula
Pto.—Puerto
Pta.—Punta
Q.—Quebrada
R.—Río, River
S.—Seno
Sa.—Sierra
Vo.—Ventisquero
V.—Volcan

NOTE: Add *s* to form plural.

Several of the maps were made from tracings by the author. The south polar projection was adapted from a National Geographic Society map (1943). The nondetailed map of southern South America and the world projection map were adapted from the Goode Base Map Series, University of Chicago. The two different types of detailed maps of southern South America were adapted from several U.S. Naval Oceanographic Office charts.

III. TAXONOMIC CHARACTERS AND MORPHOLOGY

The genus *Clasmatocolea* has a great abundance of taxonomic criteria. For the most part, traits are expressed in several or all taxa, either characterizing a distinct group or the entire genus. However, at least in my experience, *Clasmatocolea* is unique—I have not previously encountered a genus of hepatics with this magnitude of single exceptions to a general pattern of morphology. There are, in fact, *ten* instances of a morphological feature present in only o ne species of the genus. Although I cannot account for this phenomenon, it does appear that there has been considerable experimentation in the evolutionary history of *Clasmatocolea*. These deviations will be pointed out in the following discussions of the various morphological characters.

Slime papillae.—In *Clasmatocolea*, slime papillae are very common and

widespread in their occurrence. They are frequently associated with underleaves, bracts and bracteoles, terminating segments and armature, or sessile on the apex or lamina margins. I have not found slime papillae on leaves. In undivided underleaves, they are commonly present in the position of segments or teeth, representing vestigial lobes or teeth. In this connection I have seen, in several taxa, regular reduction sequences of underleaf *apices*, from segments to teeth to remnant slime papillae. The slime papillae on the underleaves serve to protect the apical meristem from desiccation, whereas those associated with bracts, bracteoles, and perianth lobes likely protect young gynoecia from desiccation during their development. Slime papillae are also common on lobules of androecial bracts where they prevent desiccation of the developing and mature antheridia as well as provide moisture important for survival of the spermatozoids, particularly since the androecia are so often intercalary in this genus.

Branching.—Within *Clasmatocolea*, branching is of major taxonomic and phylogenetic significance. From the outset of this study I have been fascinated by the interrelationships and specialization of branching patterns in this genus. My study of branch types is based upon detailed examination of numerous different collections of each species. Of particular interest is the association, to a rather significant degree, of generalized branching patterns with more primitive taxa and specialized branching with more derived species.

In Table 1, I have arranged taxa with regard to branching patterns, from the primitive condition of general, less restricted branch types to the advanced one, with localization and restriction of branch types. If one compares this table with the "Conspectus of Taxa" (p. 38), which is arranged phylogenetically, there is considerable correlation (see also fig. 1, p. 22). For example, within Subg. *Clasmatocolea*, the very general branching pattern of *C. marginata* correlates with the polystraty and four-stratose antheridial stalks, features I regard as primitive in the genus. Other examples may be drawn from Sect. *Clasmatocolea*. *Clasmatocolea moniliformis* has almost entirely ventral-intercalary branching and, at the same time, has a specialized leaf insertion unique to the genus, plus consistently undivided underleaves. *Clasmatocolea crassiretis* has a derivative branching pattern, being totally without terminal branching; the species has several other derivative features, a few of which are: (a) small, undivided underleaves; (b) terete perianths, which have virtually lost all trace of keels or wings; and (c) nodular or maximally protuberant trigones. *Clasmatocolea fasciculata* is an interesting paradox in branching. Although the species has the most generalized branching mode, even possessing *Acromastigum*-type branching (which to my knowledge is unique in

TABLE 1. Branching patterns in *Clasmatocolea*, arranged with taxa having more generalized, less restricted branch types (top) to taxa with localization and restriction of branch types.

Taxon	Branch type			
	Terminal		Intercalary	
	Frullania	Acromastigum	Ventral	Lateral
C. fasciculata	++	+	+++	+++
C. marginata	+++	0	+++	+++
C. ctenophylla	+++	0	++	+++
C. fulvella	++	0	+++	+++
C. humilis	++	0	+++	+++
C. trachyopa	+++	0	+	+++
C. strongylophylla	+++	0	++	+
C. rigens	+++	0	+	++
C. verrucosa	+++	0	+	++
C. vermicularis	++	0	+++	+
C. navistipula	+	0	++	+++
C. puccioana	+	0	+	+++
C. gayana	+++	0	0	+++
C. obvoluta	+++	0	0	+++
C. cucullistipula	+++	0	++	0
C. moniliformis	+	0	+++	0
C. notophylla	0	0	+++	+++
C. crassiretis	0	0	++	+++
C. minutiretis	0	0	+++	++
C. tjiwideiensis	0	0	++	0

0 = branch type absent; + = branch type rare; ++ = branch type occasional; +++ = branch type common.

Lophocoleaceae), it has gynoecia restricted to short, ventral-intercalary branches, a markedly derivative feature. *Clasmatocolea minutiretis*, which has no terminal branching and only occasional lateral-intercalary branching, has several other derived/specialized features, among them the most reduced underleaves of the section, and the specialized, laterally fused androecial bracts.

Other subgenera show equally intriguing correlations. *Clasmatocolea cucullistipula* (Subg. *Plicaticalyx*, see fig. 1), for example, has somewhat specialized branching, with predominantly *Frullania*-type and only occasionally ventral-intercalary type, but totally lacks the lateral-intercalary type. I regard this species as the most derived of the genus; it has, among several other specialized features: (a) contracted, plicate perianths that are often subterete toward the base and (b) androecia wider than the main axis.

Clasmatocolea notophylla (Subg. *Squamicalyx*, fig. 1) commonly has

intercalary branches of both kinds but lacks terminal branching; it also has several other specialized features, a few being (a) underleaves and bracteoles connate on both sides and (b) scaly, terete perianths without keels or wings.

There are other forms of branch specializations within the genus. *Clasmatocolea fulvella* (Subg. *Clasmatocolea*), for example, has a system of short, abbreviated intercalary branches that are vermiform and submoniliform and appear quite differentiated from the main axis (fig. 43-1). Other patterns may be observed in Subg. *Metaclasmatocolea*. In one species, *C. puccioana*, the copiously produced lateral-intercalary branches are highly differentiated—being usually abbreviated and of limited growth and having underleaves inconspicuous, reduced, and scalelike (fig. 49). In one variety of the other species of this subgenus, *C. navistipula* var. *navistipula*, a flabellate branching pattern has developed (fig. 53). These two species fall adjacent to one another in Table 1, both having nearly identical branching types, with lateral-intercalary type common, ventral-intercalary rare or occasional, and terminal branching rare.

Stems.—The stem anatomy is quite species specific and is usually a useful supplementary character. *Clasmatocolea* taxa may be divided into four groups based upon stem anatomy:

Group 1.—Stems with moderate to distinct differentiation, having a cortex of 1-2(-3) rows of thick-walled cells *equal to or smaller* than the medullary. The stems are 5-18 cells high. Eight taxa are in this group; examples are *C. fasciculata* (fig. 26-5), *C. puccioana* (fig. 49-4), and *C. fulvella* (fig. 43-15). None of the diminutive taxa of the genus fall here.

Group 2.—Stems with moderate to distinct differentiation, having a cortex of *one* row of thick-walled cells *larger* than the medullary. All of the species are diminutive for the genus, and all have stems between four and seven cells high. All species referable here are of Sect. *Clasmatocolea: C. strongylophylla* (fig. 46-5, 6), *C. crassiretis* (fig. 36-10), and *C. ctenophylla* (fig. 34-14).

Group 3.—Stems with virtually *no internal differentiation* and consisting of very thick-walled cells. The stems are 6-9 cells high. Here belong *C. gayana* (fig. 31-9), *C. minutiretis* (fig. 40-7), *C. tjiwideiensis* (fig. 48-10), and *C. cucullistipula* (fig. 57-3).

Group 4.—Stems with the slightly to distinctly thickened cortical cells variable: *smaller, equal to, or larger* than the medullary cells and thus not fitting into any of the above groups. Species in this group commonly have a smattering of several large and small cells in both cortex and medulla. The stems are 5-10 cells high. Belonging here are species from four sub-

genera—*C. rigens* (fig. 7-5), *C. trachyopa* (fig. 14-5), *C. moniliformis* (fig. 38-10), and *C. navistipula* (fig. 52-30).

Endophytic hyphae.—Fungal hyphae, at least some of which are of basidiomycetes (verified by the presence of clamp connections), are present in a number of *Clasmatocolea* species. When present, the endophytic hyphae occur in both cortical and medullary cells of the stem. This feature does not seem to be of taxonomic significance.

Rhizoids.—Within the genus *Clasmatocolea*, rhizoids are rather uniform, but several points of interest deserve mention. As in other Lophocoleaceae, rhizoids are in fascicles from the stem near the underleaf base. However, in addition to this position, *C. tjiwideiensis* also has them from the stem adjacent to the ventral base of leaves, and, in *C. cucullistipula*, the rhizoid field includes the median basal portion of the underleaf lamina (fig. 57-1). In *C. gayana*, rhizoids issue from a raised, flat, disciform rhizoid initial field (fig. 31-8 and p. 116 for discussion), a feature I find useful in assisting identification of the species. The rhizoid tips are simple or branched and are colorless, except in *C. tjiwideiensis*, where they are, remarkably, magenta.[1] At least in some instances, the rhizoid tips branch in "response to contact with a solid substratum" (see Odu & Richards, 1976, for a discussion of this phenomenon in *Lophocolea cuspidata*).

Leaves.—Compared with many other groups of hepatics in which the major focal point of evolution seems to have been foliar structures, the leaf in *Clasmatocolea* is at best of moderate phylogenetic and taxonomic significance. Pronounced exceptions are taxa with divided leaf apices, namely those taxa in Subg. *Protoclasmatocolea* and Subg. *Lacerifolia*. Within these two allied subgenera, there is a trend that reaches a culmination in degree of complexity in *C. trachyopa*. No other species in the genus, for example, has the intricacy of folding and armature; no other species has three-lobed leaves or accessory lobes at the leaf apex and margins (see figs. 14, 15).

In the remaining bulk of taxa, *i.e.*, those with undivided leaf apices, the leaf, though often distinctive for the species, shows remarkably little morphological diversity. Several taxa, in an array of diverse sections and subgenera, have leaves distinctly conchiform concave, oblate to wide ovate (and variations of these) in shape, entire, with the dorsal margin straight (at least in proximal half), and the ventral margin broadly rounded. However, within the undivided leaf group, generally when the leaf is armed it is of greatest taxonomic use. For example, the sinuate main axis

[1] See Schuster & Engel (1977) for a discussion of the taxonomic value of claret-red (magenta) vs. colorless rhizoids in the genus *Schistochila*.

leaves of *C. fulvella* (fig. 43-1), the distinctive position of the teeth in *C. tjiwideiensis* (fig. 48), the sharp, often strongly incurved teeth of *C. minutiretis* (fig. 40), and notably, the dentition of the beautiful, diminutive, *C. ctenophylla* (fig. 34).

Leaves of *Clasmatocolea* are unistratose throughout in all species save one—in *C. marginata*, polystraty has developed in the leaf margins and the median-basal portion of the leaves.

Leaf cells and oil-bodies.—The form of the leaf cells in *Clasmatocolea* is somewhat variable. Leaf cells are thin to moderately thickened except in *C. moniliformis* where walls are distinctly thickened. Even though trigones for the most part are large and bulging to occasionally coarse and nodular, the deviations from this condition are not only taxonomically significant but possibly of some evolutionary significance. Minute trigones occur in the simple, most primitive member of the genus, *C. rigens*. Further, small trigones are also present in *C. marginata*, which likewise has several primitive features. The only other instance of trigones being absent or small is in *C. vermicularis;* this condition is useful, incidentally, in separating this species from all other members of Sect. *Clasmatocolea*. In four, mostly unrelated, derivative taxa—*C. crassiretis*, *C. notophylla*, *C. verrucosa*, and *C. cucullistipula*—the trigones are massive, as well as nodular and protuberant to the extent that the cell lumen is bounded, except for a few narrow, thin-walled places, mostly by trigones (cf. figs. 36-9, 55-9, 57-2). I regard this condition as derivative. The development and consistency of trigones shows a sharp divergence from the genus *Lophocolea*. It appears that this trend has gone from absent or minute trigones to the massive condition just discussed.

The cuticle is mostly smooth or slightly roughened, but has been used as a criterion for Sect. *Strongylophyllae*, which has coarse, hemispherical-oblong papillae (fig. 46-7). *Clasmatocolea verrucosa* is unique in possessing huge, domelike verruca, one per cell.

In general, cell size is of minor importance. In *Clasmatocolea*, although I have used cell size as an aid in separating "look-alikes," I have not used cell size as a key character.

Oil-bodies are known for six of the species. In general, they are of the grape-cluster type, with the surface appearing granular or papillose or botryoidal, and are consistently 2 or 2-3 per cell in the leaf middle and occupy only a small fraction of the cell lumen. *Clasmatocolea moniliformis* is a noteworthy deviant, having oil-bodies occupying 0.20-0.75 of the cell lumen but with them absent from marginal rows of leaf cells. All data of oil-bodies are from personal observations, except that for *C. vermicularis*, which I have obtained from Gradstein et al. (1977).

Underleaves.—The majority of species of *Clasmatocolea* have very characteristic underleaves that are of high taxonomic value. Many and various underleaf characters have been utilized taxonomically in the genus.

The underleaves vary from the highly reduced, plane, deeply bifid individuals, which are maximally 0.6 × the stem width in *C. minutiretis*, to the large, cucullate, undivided structures, which are maximally 6.7 × the stem width in *C. moniliformis*. Many intermediates, with various combinations of characters, fall within these extremes.

The underleaf width vs. the stem width, a comparatively stable feature, has frequently been used; the following are some examples: (a) *C. minutiretis* (which culminates a reduction sequence in Sect. *Clasmatocolea*) has underleaves only 0.35-0.6 × the stem width; (b) *C. vermicularis* has underleaves normally slightly narrower than the stem, a very useful species criterion; and (c) *C. moniliformis*, with the very large underleaves mentioned above. In this connection, mention should be made of the highly reduced, scalelike underleaves of the main axis and/or branches of Subg. *Metaclasmatocolea;* underleaves of *C. puccioana* and *C. navistipula* here provide critical criteria pertinent at the subgeneric level.

Convexity and associated manifestations are a useful tool, helping to define many taxa, a few of them being (a) *C. fulvella*, with inflated, orbicular cucullate branch underleaves (fig. 43); (b) *C. moniliformis* and *C. notophylla*, each with distinct cucullate underleaves (fig. 38); and (c) *C. cucullistipula*, with cucullate, auriculate underleaves (fig. 57). Very different from this condition are the plane underleaves of *C. crassiretis* (fig. 36) and of *C. minutiretis* (fig. 40).

Lamina armature is useful in circumscribing and identifying such species as *C. fasciculata*, with its single, large lacinium (fig. 25), and *C. cucullistipula*, with its single, large lobe extending above the dorsal stem surface (fig. 57).

In nearly all species, the underleaves are either undivided or bifid to less than 0.5, but in *C. minutiretis* they are bifid to 0.7, and in *C. rigens* they are usually bifid to nearly the base.

In the majority of taxa, the underleaves are free or connate on one side, but in four mostly unrelated species they are connate on both sides—*C. obvoluta*, *C. tjiwideiensis*, *C. notophylla*, and *C. verrucosa* (cf. fig. 55).

Underleaves are usually transversely inserted, but the frequently oblique insertion in *C. rigens* is usually the first character I search for in identifying this species.

Androecia.—Within *Clasmatocolea*, androecia are strongly differentiated from leaves. The bracts are distinctly saccate or ventricose in the basal

half, whereas the distal portion is strongly concave. The androecial region, then, is markedly narrower than neighboring sterile portions of the axis, except in one species, *C. cucullistipula*, in which the androecial region is distinctly wider (fig. 58-8).

The specialized, certainly derivative, laterally fused androecial bracts are exceptional in the genus and occur in three species (figs. 14-6 and 41-9). They are present in both species of Subg. *Lacerifolia*, where I have used the character taxonomically, not only as an aid to circumscribing the subgenus but in separating it from the allied Subg. *Protoclasmatocolea*. Fused bracts appear again in the quite unrelated *C. minutiretis*, a derivative species in Subg. *Clasmatocolea*.

Compared to Lophocoleoid androecial bracts I have studied, the lobules in *Clasmatocolea* are large in proportion to bract size (see p. 83). In all species but one, the lobule is a flap of tissue formed by dilation and infolding of the dorsal base of the bract (figs. 28-15, 41-10). The exception is *C. navistipula*, which has conduplicately bilobed bracts (fig. 53-10, 11), a condition quite unusual for hepatics. The lobules in *Clasmatocolea* are usually incurved to involute, with the margin entire or sparingly dentate with few-celled teeth and/or with one lacinium or a single, commonly involute lobe; lobule margins nearly always have slime papillae. The armature of *C. cucullistipula* is somewhat unusual in having 1-3 laciniae or small lobes (fig. 58-9, 10).

The antheridia are solitary, only rarely occurring two per bract. Antheridial stalks are uniseriate throughout or commonly with localized bistratose areas (figs. 12-5, 28-11); in no case are they bistratose throughout. Stalks are four-seriate in *C. marginata* (fig. 18-12).

Bracts.—With the exception of size, the bracts do not deviate to any major extent from the leaves. Those species with divided leaves also have divided bracts (bifid, except in *C. trachyopa*, where often trifid), whereas those taxa with undivided leaves have undivided bracts. However, bracts are occasionally short-bifid in *C. humilis* and *C. gayana*, species in which the leaves are always undivided. With the conservative nature of the gynoecium in mind, perhaps the presence of at least some bifid bracts in taxa with undivided leaves is meaningful in a phylogenetic context, indicating a bifid-leaved ancestry.

Almost without exception, taxa with armed leaves have armed bracts, whereas those with entire leaves have entire bracts. For the most part, the amount and magnitude of armature is expressed to a greater extent on bracts as compared to leaves (figs. 58-1 and 41-1). Armature is commonly

expressed on the bract apex and upper margins and to a considerably lesser extent on their median and basal portions.

Bracteoles.—The innermost series of bracteoles are conspicuous, considerably larger than, and, in most instances, clearly differentiated from, underleaves. These features of the bracteole at once set the genus *Clasmatocolea* apart from the genus *Hepatostolonophora.*

Bracteoles are differentiated from underleaves by modification of several features, as outlined below:

Size.—In nearly all cases, bracteoles are markedly larger than underleaves. In fact, in seven instances, bracteoles are subequal to the bracts in size, even though these species have a considerable gap in leaf and underleaf size.

Apical division.—In nearly all species with divided underleaves, the bracteoles are less deeply incised or even undivided. This reduction is often accompanied by an alteration in shape and magnitude of segments.

Armature.—In nearly all species, the amount and magnitude of bracteole armature is significantly increased over that of the underleaves.

Convexity.—Underleaves are, in ventral view, plane or convex, but in many instances, the bracteoles are, in ventral view, concave to canaliculate (see fig. 23-5).

Connation.—With one exception, bracteoles are free from bracts even though, in many cases, the underleaves are connate with leaves on one side. Absence of bracteole connation is likely due to secondary meristematic activity in the region of the perianth, thus spacially displacing bracteole and bract. The exception noted above is *C. notophylla*, which has bracteoles (conspicuously) connate with the bracts on both sides. See plates of *C. minutiretis* (figs. 40, 41) for illustrations of most of these modifications.

Perianths.—This structure, including position, shape, and lobe features, is of considerable taxonomic significance within the genus *Clasmatocolea.* Perianths are strongly trigonous to distinctly terete and have three broadly rounded, entire or variously armed, sometimes bifid lobes, the latter occurring only within the two most primitive subgenera (see discussion below). In general, as to be expected, those species with entire leaves will have entire perianth lobes, whereas those plants with armed leaves will have armed perianth lobes. Usually the character of armature will be expressed to a greater and more reliable extent on perianth lobes than on leaves. Several species may be immediately recognized by their taxonomically useful, characteristic perianth mouth and lobes; a few examples

follow. *Clasmatocolea vermicularis* has perianth mouths wide and open and lobes entire[2] and often deeply cleft (figs. 28-16, 29-2, 4); *C. gayana* has perianths with the mouth region bilaterally compressed and has lobes densely denticulate (figs. 31-1, 32-5, 6); *C. ctenophylla* has numerous, 1-2-celled, sharp teeth that are more or less *equal in size* (fig. 34-15, 16); and *C. cucullistipula* is unique in having perianths contracted at the mouth (fig. 58-1) and plicate toward the apex (fig. 58-1, 4, 5).

The trigonous, "Epigoniantheae"-type of perianth is generally regarded to have arisen from a terete perianth or "urn-shaped cup" (see Schuster, 1966, incl. fig. 52, and Fulford, 1965). Within *Clasmatocolea*, the primitive condition is characterized by a sharply trigonous perianth with each of the three lobes bifid, reflecting the nature of the foliar structures from which they originated. Further, the points of fusion of the leaves are frequently delineated by the presence of wings (fig. 31-1, 2), which are not only a remnant, but a reminder, of the origin of the perianth from leaves. The combination of strongly trigonous perianths with bifid lobes and winged keels occurs only in the two most primitive subgenera—Subg. *Protoclasmatocolea* and Subg. *Lacerifolia*.

The question then arises of the occurrence and significance of terete perianths in *Clasmatocolea*. In *all* of the more advanced taxa of the genus (*i.e.*, all taxa except Subg. *Protoclasmatocolea* and *Lacerifolia*), the perianth lobes are broadly rounded, the bifid condition having been lost. Further, in some taxa there has been a loss of distinct keels and, at the same time, of wings, and it is in these taxa that the terete perianth condition has developed. This leads me to the conclusion that the terete condition in *Clasmatocolea* is a secondarily derived one. Terete perianths occur in such derivative taxa as *C. notophylla* (Subg. *Squamicalyx*, fig. 55-2), *C. cucullistipula* (Subg. *Plicaticalyx*, fig. 58-1, 6), *C. strongylophylla* (Sect. *Strongylophyllae*), and *C. crassiretis* (Sect. *Clasmatocolea*, fig. 36-3). A subterete condition also occasionally occurs in *C. vermicularis* (Sect. *Clasmatocolea*, fig. 28-16). It should be brought out that, for the most part, the occurrence of terete perianths is linked with a substantial reduction in size of the ventral lobe (fig. 36-3), another feature supportive of the derivative nature of the terete perianth.

The reduction of the ventral perianth lobe mentioned above has sometimes been accompanied by a suggestion of bilateral compression. This

[2] Grolle (1956) recognized only a single species in *Clasmatocolea*, *C. heterostipa* (= *C. vermicularis*), and used the wide, entire perianth mouth of that species to assist in distinguishing the genus. Later, in Grolle (1960), however, the genus assumed a much larger size, and this character became meaningless.

kind of condition is of some significance, for it suggests the connection to the *Leptoscyphus* type of perianth (see Schuster, 1966, p. 552) and supports, along with several other features, a relationship between *Clasmatocolea* and *Leptoscyphus* (see also p. 26).

In the majority of *Clasmatocolea* taxa, there is a well-developed and distinct perianth along with a true calyptra, without development of a stem perigynium. However, vestigial stem perigynia have independently developed in a wide variety of unrelated taxa. In this condition, there is a swollen region of axial proliferated tissue at the perianth base on which several or all of the bracts and bracteoles are inserted. Vestigial shoot perigynia are feebly developed in *C. vermicularis* and *C. ctenophylla*, more so in *C. navistipula*, and appear to reach an optimal extent of development for the genus in *C. puccioana* (fig. 50-1).

With greater axial proliferation, along with formation of a shoot calyptra, a coelocaule precursor has developed in Subg. *Lacerifolia* (fig. 12-1). Here, the sporophyte "penetrates" to about the level of bracts of the first series or the leaves immediately below. The coelocaule precursor developed in *Clasmatocolea* is quite comparable to that in the genus *Temnoma* (see Schuster, 1967) and that referred to by Schuster (1966) as the "*Temnoma* subtype" of axial protection of the embryo. More specifically, the coelocaule precursor in *Clasmatocolea* is similar to less extreme forms of the *Temnoma* subtype; compare for example Figure 53-4 in Schuster (1966) for *T. palmatum*, and Figure 11-1 for *C. obvoluta*. As in *Temnoma*, there is likely minimal actual penetration of the sporophyte into axial tissue, but rather a proliferation of axial tissue upward in a cylinder around the developing sporophyte. The bracts and bracteole, as in *Temnoma*, are widely separated.

Setae.—The seta exhibits no sharp internal differentiation when observed in transverse section. The epidermal layer is smaller than, equal to, or larger than the scattered, rather numerous internal cells, with little or no correlation of relative size and taxonomy. The number of cells in the epidermal row varies from 14 in *C. cucuillstipula* to as many as 70 in *C. humilis*. Other features also vary, such as the number of cells in seta diameter, as well as trigone-like thickenings of epidermal and inner cells. See the key to sporophyte material (p. 20).

Capsules.—These structures are variable in shape, but in no case are acute or beaked capsule tips developed (such as those in Acrobolbaceae and Schistochilaceae). Capsule walls are 3-6-layered, often with some variation of layer number on the same valve. The outer layer is always thicker, equivalent to 1.8-3.9 of the interior strata. An extreme is reached

in *C. minutiretis*, where the outer layer of cells exceeds the thickness of all the interior strata combined (fig. 41-7). The outer layer not only has nodule-like to spinelike thickenings on radial walls, but varying amounts of semiannular bands that extend from radial onto tangential walls (fig. 34-13). Only in *C. vermicularis* and *C. humilis* are semiannular bands lacking on the outer layer. The intermediate capsule wall layers are fairly uniform in wall features and possess tangentially dilated thickenings on radial walls. For the most part, the intermediate and inner layers are subequal in thickness. In a few species (*C. navistipula* and *C. puccioana*), the outermost *intermediate* layer is thicker than the innermost layer of the *capsule*. The inner layer of cells has semiannular bands extending from radial onto tangential walls. In several species, these bands are often incomplete. The radial walls often have nodulose thickenings interspersed with the bands. Except for the presence of semiannular bands in the outer layer, the type of capsule wall in *Clasmatocolea* fits the *Jungermannia* type outlined in Schuster (1966).

Grolle used capsule wall anatomy as a generic criterion. Grolle (1956) thought *C. heterostipa* had a bistratose capsule wall that, along with the wide mouth and entire lobes of the perianth, was regarded as generically diagnostic. Grolle (1960), however, eliminated this feature and substituted for it the presence of "knotigen bis halbringförmig" thickenings in the inner capsule wall layer as a generic criterion. The type of wall thickening found in *Clasmatocolea* needs evaluation and comparison with a wide array of other austral *Lophocolea;* this topic is currently under investigation.

Spores.—Within *Clasmatocolea*, there are two, narrowly circumscribed, yet very different spore types.

Type 1.—Spores densely granulate, grading to short, wide, irregular vermiform ridges, which are covered (often densely so) with nanogranules (pls. 10, 25).[3] The great bulk of *Clasmatocolea* taxa have this spore type. Spores in this category are 10-18 μ, reaching an upper limit in *C. vermicularis*, where they are 15-20 μ. This type of spore is surely primitive within the genus. In general, as to be expected, species with larger spore size have a greater spore-elater diameter ratio.[4] For example, *C. vermicularis* has spores 15-20 μ and a spore-elater ratio averaging 1.9 :1, whereas *C. obvoluta*, with spores 11-12 μ, has a ratio averaging 1.1 :1. However, *C.*

[3] I have used the term "nanogranule" in the sense used by Sorsa & Koponen (1973) in their studies of Mniaceae spores.

[4] In *Clasmatocolea*, as in many groups of Hepaticae, the direct correlation between spore size and spore-elater ratios is due to the relatively small elater width variation.

rigens is an interesting exception to the rule, with spores 14-18 μ and a spore-elater ratio averaging 2.4:1. *Clasmatocolea obvoluta* and *C. pucciona, both with spores 11-12* μ, form an interesting contrast: the former has a spore-elater ratio of 1.1:1 and the latter, 1.5:1.

Type 2.—Spores with elongate, narrowly conical or subrectangular projections. Within this derivative spore type there is a trend in specialization of the projections, culminating in strongly dilated, clawlike tips (pls. 28, 29). This type of spore is represented in but three species—*C. cucullistipula*, *C. ctenophylla*, and *C. gayana*—belonging to two distantly related subgenera. Within these taxa, it appears that the presence of this spore type has ecological rather than phylogenetic relevance. The only instances of elongate projections of the exine are in corticolous members of the genus, and it is certainly possible that this spore type is useful in facilitating establishment of these plants. Two taxa in this group have the largest spores in the genus—*C. gayana*, with spores 21-24 μ, and *C. cucullistipula*, with spores 24-27(-30) μ, with the latter also having the largest spore-elater diameter ratio in the genus, 2.8:1. The greater surface area of the very large spore of *C. cucullistipula may* be of significance in anchorage and establishment of the spore in the unique and interesting niche of the species—loosely adhering to or semipendent from very small branches or twigs. The third species, *C. ctenophylla*, has much smaller spores, being 12-15 μ.

Scanning electron micrographs of spores of *Clasmatocolea* may be found on pages 204 through 224.

Elaters.—I have not found elaters to be of phylogenetic or taxonomic value in *Clasmatocolea*. These structures in *Clasmatocolea* are bispiral and taper gradually toward the ends. Some species are spiraled to the tips, whereas others often have apices with a thick, nonspiral wall, which does not seem to be of taxonomic significance. Elaters are 6-12 μ in diameter, with elater walls 2-5 μ wide.

IV. COMPARATIVE MORPHOLOGICAL DIVERSITY AND EVOLUTION OF SPOROPHYTE AND GAMETOPHYTE

From the beginning of this study I have been interested in determining if there are trends, relationships, or correlations of sporophyte characters that reflect evolutionary tendencies in the gametophyte. It is apparent that the few trends and character correlations present in the sporophyte generation reflect the stature of the gametophyte or ecology rather than any evolutionary trends in the gametophyte. For example, diminutive species such as *C. ctenophylla*, *C. cucullistipula*, and *C. navistipula* tend to

have a reduced seta, both in number of cells in seta diameter and in epidermal row. It is apparent, after examining characters available from the sporophyte and the gametophyte, that morphological diversity and amount of evolution are vastly different in the two generations of *Clasmatocolea*. To underscore this, one need only to compare the preceding discussions of taxonomic characters found in the gametophyte and sporophyte generations. These findings are certainly not unexpected, for the persistent gametophytes and the ephemeral sporophytes have entirely different selective pressures acting upon them. See Schuster (1966) for a lengthy discussion of these factors.

In an attempt to assess the overall taxonomic value of the sporophyte and the diversity of its characters, I have constructed a key, based solely on sporophyte material, but with spore and elater data added. To evaluate the variability of characters as well as to minimize risks that accompany inadequate sampling, a number of sporophytes of each species were studied whenever possible. For example, ten sporophytes of *C. trachyopa* were studied in detail.

ARTIFICIAL KEY TO TAXA BASED UPON SPOROPHYTE MATERIAL

1. Spores averaging more than 1.5 × the elater diameter....2
   2. Spore wall with elongate, narrowly conical, or subrectangular projections....3
      3. Spores 12-15 μ; capsule wall 3-4 layers thick....*C. ctenophylla*
      3. Spores 21-27 μ; capsule wall 4-5 layers thick....4
         4. Elaters 8-10 μ; outer capsule wall layer with semiannular bands very common....*C. cucullistipula*
         4. Elaters 10-12 μ; outer capsule wall layer with semiannular bands few....*C. gayana*
   2. Spore wall granulate grading to short vermiform ridges....5
      5. Spores averaging 2.4 × elater diameter....*C. rigens*
      5. Spores averaging 1.9 × elater diameter....6
         6. Capsule wall 3-4 layers thick; outer capsule wall layer without semiannular bands, the wall equal to 2 of interior strata; capsule oblong to globose *C. vermicularis*
         6. Capsule wall 4-5 layers thick; outer capsule wall layer with semiannular bands, the wall equal to 2.5-3 of interior strata; capsule broadly ovate to elliptic....*C. fulvella*
1. Spores averaging 1.5 × or less the elater diameter....7
   7. Spores averaging 1.1-1.2 × elater diameter....8
      8. Outer capsule wall layer exceeding all of interior strata combined....*C. minutiretis*
      8. Outer capsule wall equal to 2-3 of interior strata....9
         9. Seta with 30-70 rows of outer cells; outer capsule wall layer without semiannular bands....*C. humilis*
         9. Seta (where known) with 19-32 rows of outer cells; outer capsule wall layer (of at least some valves) with semiannular bands....10
            10. Capsule wall 36 μ thick, of 4 layers....*C. strongylophylla*
            10. Capsule wall 30-72 μ thick, of 4-6 layers....*C. obvoluta*

7. Spores averaging 1.4-1.5 × elater diameter 11
11. Outer capsule wall layer equal to 1.8-2.5 of interior strata ..... *C. trachyopa*
11. Outer capsule wall layer equal to 3-3.9 of interior strata 12
12. Seta with 15-16 rows of outer cells; capsule wall 36-42 μ thick ..... *C. puccioana*
12. Seta with 28-33 rows of outer cells; capsule wall 42-48 μ thick ..... *C. navistipula*

V. ORIGIN OF CLASMATOCOLEA AND SOME EVOLUTIONARY TRENDS

I believe that the genus *Clasmatocolea* arose from a simple member of the genus *Lophocolea*, characterized by such features as (a) convex, shallowly bifid, longer than wide leaves; (b) deeply bifid, rather large underleaves; (c) a plastic branching pattern without restriction of terminal or intercalary branches; (d) branches both like one another and like the main axis; (e) a simple, sharply trigonous perianth, with the three lobes bifid; (f) bracts and bracteoles bifid, much like the leaves; and (g) absence of any secondary pigments. Further, I postulate a Southern Hemisphere origin of the genus from an ancestor similar to a dioecious *Lophocolea lenta* (a monoecious taxon of southern Chile and the Falkland Islands), a species possessing many of the features listed above. From this pool of *Lophocolea lenta*-like plants, I believe there was an evolutionary line in which there had been an alteration of leaf concavity, seemingly a simple change, leading from a convex leaf to a concave one. Such plants might resemble *Clasmatocolea rigens*, also of the southern South American sector and the most primitive member of the genus.

From this hypothetical prototype of *Clasmatocolea*, I believe early evolution occurred along two basic lines, both quite divergent from *Lophocolea*—one line toward Subg. *Protoclasmatocolea* and Subg. *Lacerifolia*, both with divided leaves, and the other toward the remaining groups, all of which have undivided leaves (see fig. 1).

The Subg. *Protoclasmatocolea-Lacerifolia* line is an intriguing one, progressing from the basic, simple, shallowly bifid leaf of *C. rigens*, to species with an increasing elaboration and specialization of the leaf. This trend can be observed proceeding from *C. rigens*, to the still simple *C. obvoluta* var. *cookiana*, to the more complex *C. obvoluta* var. *obvoluta*, to the complicated, intricate leaves of *C. trachyopa*, which terminates the line.

From the larger pool with undivided leaves, there is an offshoot comprising Subg. *Clasmatocolea* (see fig. 1). This line, in turn, has several offshoots, each leading to a specialization of one or more structures, such as elaboration of branching and underleaves (Sect. *Fulvellae*) or elabora-

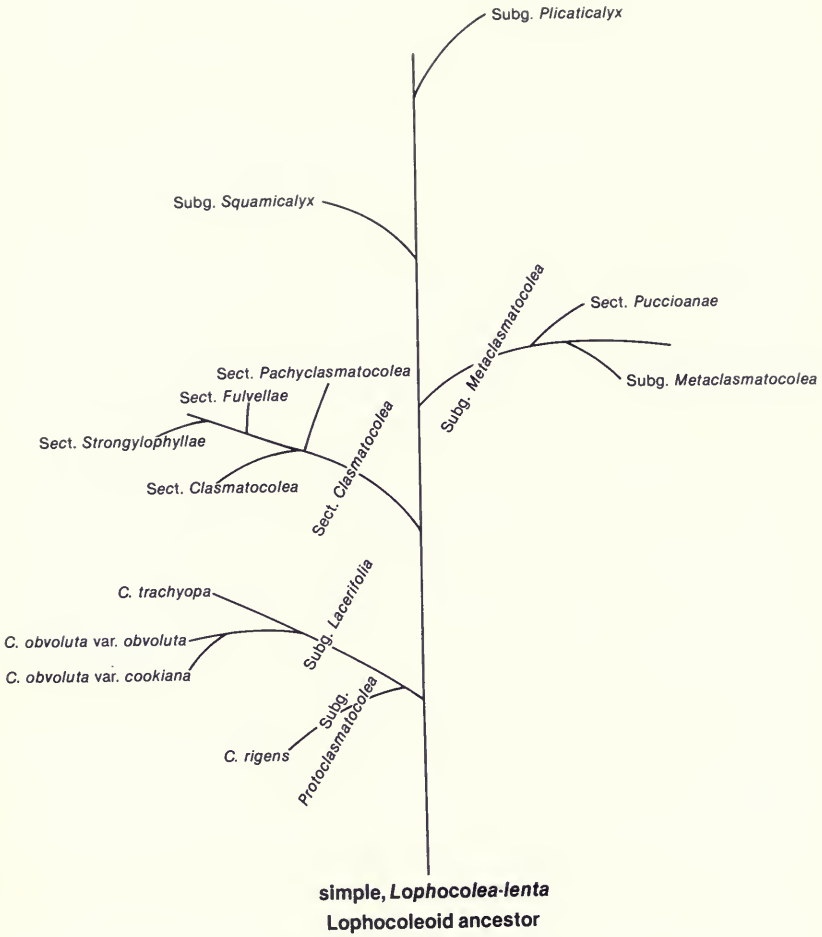


FIG. 1. Diagrammatic representation of suggested major evolutionary lines in *Clasmatocolea*.

tion of the cuticle (Sect. *Strongylophyllae*). Another offshoot takes in the largest section of the genus, Sect. *Clasmatocolea*. There are some interesting trends within this section; some are isolated evolutionary experiments that are present in but a single species, whereas other trends are sequential, encompassing all taxa within the section. Some of these trends are listed below.

Primitive character	*Advanced character*
Underleaves large, conspicuous	Underleaves small, inconspicuous
Underleaves divided	Underleaves retuse or undivided
Branching pattern generalized (see Table 1)	Branching pattern specialized, with 1 or more types absent
Stem anatomy generalized	Stems with differentiation of a distinct cortex
Trigones absent or minute	Trigones massive, the cell lumen bounded mostly by trigones
Rhizoid pads absent	Rhizoid pads present
Leaf insertion simple (cf. *C. humilis*)	Leaf insertion specialized (cf. *C. monilifornis*)
Perianths trigonous	Perianths terete, at least toward the base
Perianth keels present, wings well developed	Perianth keels and wings absent
Ventral lobe of perianth large, like the lateral	Ventral lobe of perianth reduced, smaller than the lateral
Spore exine with vermiform ridges	Spore exine with elongate projections

Another offshoot from the line possessing undivided leaves is Subg. *Metaclasmatocolea*, with specialized branching modalities and highly reduced underleaves. There are fascinating trends in this line, with one section (*Puccioanae*) developing a complex system of lateral-intercalary branches and having underleaf reduction only on the branches. The other section (*Metaclasmatocolea*) has developed a flabellate branching pattern and underleaf reduction on all axes, including the main one.

There are two independent and derivative lines, each quite apart from the main stream of evolution within the genus, but still within the undivided leaf group (see fig. 1). One comprises Subg. *Squamicalyx*, with such derivative features as underleaves connate on both sides (including, on one side, connation with the leaf lamina in *C. notophylla*), massive trigones that nearly surround the cell lumen, and more or less terete perianths with large, curious scales. The second line, the monotypic Subg. *Plicaticalyx*, is the most derivative, isolated taxon in the genus. Nowhere else does one find such features as contracted, plicate perianths, andreocia wider than the main axis, 2-3 laciniate-lobate androecial bracts, or distinctly auriculate underleaves.

VI. GENERIC RELATIONSHIPS OF CLASMATOCOLEA

Clasmatocolea is a discrete, well-defined genus of Lophocoleaceae closely related to *Lophocolea*, *Leptoscyphus*, *Evansianthus*, *Pachyglossa*, *Hepatostolonophora*, and *Xenocephalozia*. These genera also independently relate to other genera in the family (see fig. 2).

Several different evolutionary lines within *Clasmatocolea* show relationships to *Lophocolea*, a rather large genus with considerable species diversity in the Southern Hemisphere; some of these are outlined below:

1. *Clasmatocolea rigens* (Subg. *Protoclasmatocolea*) approaches several bifid-leaved *Lophocolea* taxa, such as *L. lenta* and to a lesser extent *L. leptantha* and *L. textilis*, all from southern South America (see related discussion on p. 21).

2. *Clasmatocolea vermicularis* (Sect. *Clasmatocolea*) has some phenotypes quite reminiscent of *L. sabuletorum* of southern South America and the Falkland Islands (see p. 104).

3. *Clasmatocolea humilis* (Sect. *Clasmatocolea*) approaches the *L. austrigena-gunniana* complex and has a similar amphipacific distribution. There are certain phenotypes of all three of these species that cause considerable taxonomic difficulty *between genera* (see discussion on p. 82).

4. *Clasmatocolea humilis* also shows a relationship, but to a lesser extent, to *L. otiphylla* of southern South America (see p. 82).

Although there are several points at which *Clasmatocolea* and *Lophocolea* are taxonomically close to one another, evolution in the two taxa has diverged sharply. For example, in the *C. rigens-L. lenta* species pair, a divergent sequence can be observed beginning with *C. rigens*, progressing through the varieties of *C. obvoluta*, and culminating in *C. trachyopa*. The simple *L. lenta*, on the other hand, relates to Lophocoleoid species with distinctly convex leaves. A different situation exists for *C. humilis* and the *L. austrigena-gunniana* complex. *Lophocolea austrigena* is part of a trend sharply diverging from evolutionary developments seen in *Clasmatocolea*, proceeding from *L. boveana* to *L. austrigena* (and its ally *L. gunniana*) and culminating in the nearly isophyllous *L. gottscheoides*, which does not, by any means, suggest the genus *Clasmatocolea*.

Divergent evolution of *Clasmatocolea* from the Lophocoleoid line seems to have involved mainly leaf characters. Leaves of *Clasmatocolea* are adaxially concave and are commonly conchiform concave, whereas those of *Lophocolea* are plane or convex. Concomitant with this, the trigones in *Clasmatocolea* are large to massive, and the cell size small; *Lophocolea* has comparatively much smaller trigones and larger cells.

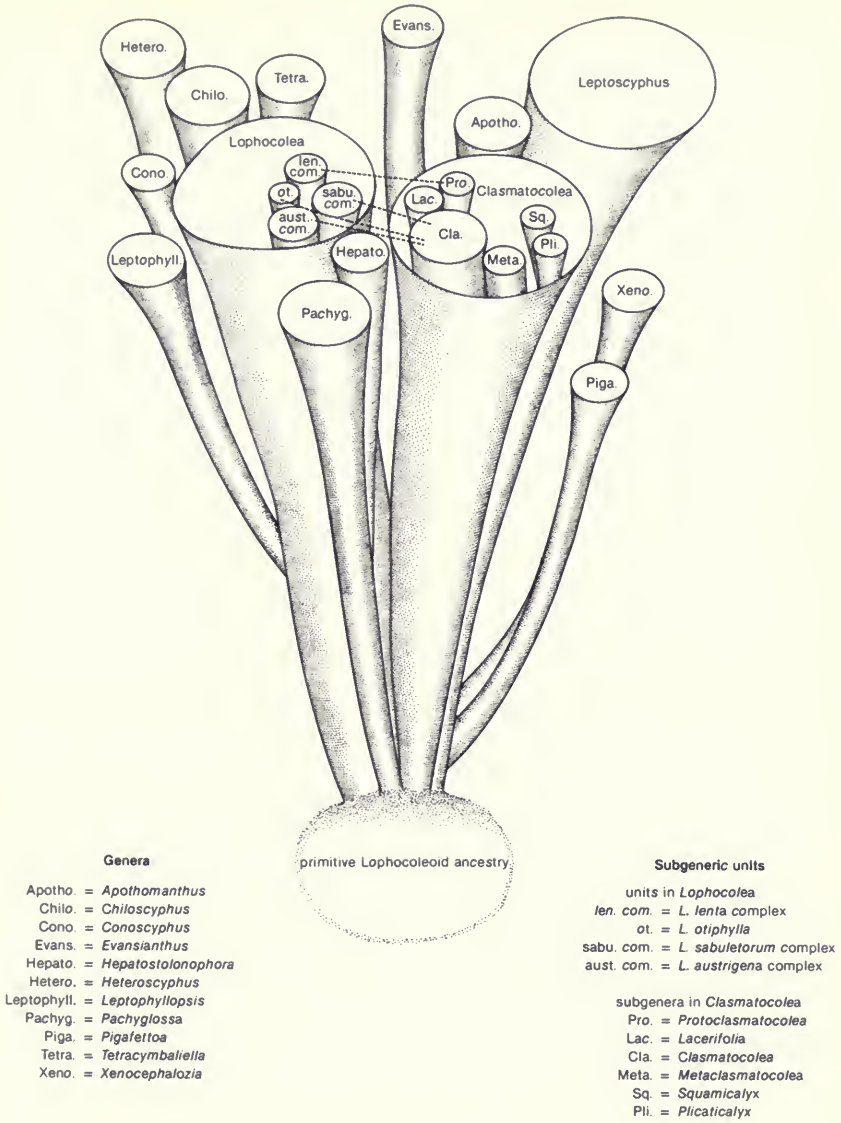


FIG. 2. Pictorial representation of generic relationships in Lophocoleaceae.

The number and significance of shared characters of *Clasmatocolea* and *Leptoscyphus* indicate an affinity between these genera; these features are outlined below:

1) In several independent lines of *Clasmatocolea*, there is a tendency for reduction of the ventral lobe of the perianth. In these groups, as well as those that have a well-developed ventral lobe, a bilateral compression of the perianth is not unusual. Such bilaterally compressed perianths are not far removed from the Leptoscyphoid perianth. Further, one should recall that there are several species of *Leptoscyphus* in which a third ventral lobe of the perianth is present, even though perianths in these taxa are strongly bilaterally compressed and remain two-lipped.

2) *Leptoscyphus* has several species that have strongly conchiform concave leaves much like those of *Clasmatocolea*.

3) Large, bulging, knotlike trigones are commonplace in both genera.

4) The texture of the plants is quite similar in the two genera.

The two genera, however, are quite independent of one another. *Clasmatocolea* lacks the ability to produce reddish pigments that is so widespread in *Leptoscyphus*. Further, trends toward perianth bilateral compression in *Clasmatocolea* notwithstanding, the shape of the perianth still may be nicely used to separate the genera—basically trigonous to terete with the ventral lobe well developed in *Clasmatocolea* and strongly bilaterally compressed, basically two-lipped in *Leptoscyphus*.

Clasmatocolea is more remotely allied to the genus *Evansianthus*, which has a similar basic plant physiognomy, including concave leaves. *Evansianthus*, however, is at once distinct from *Clasmatocolea* through possession of the following characters, which dictate a more distant relationship: (a) well-developed bilaterally compressed perianths; (b) *Andrewsianthus*-type branching; (c) presence of flagella; and (d) subterranean habit of growth. See Schuster & Engel (1973) for further notes on *Evansianthus*.

Clasmatocolea is allied to the genus *Pachyglossa*, although evolution in the two genera seems to have gone in different directions. I regard *C. marginata* as pivotal in connecting these two genera. This species is erect, rigid, brown pigmented, has polystratose leaves and underleaves (at least in the basal region), and has well-developed intercalary branching—all of which are features of *Pachyglossa*. I found the apical portions of robust axes of *C. marginata* particularly striking, for they have much the facies of an overblown *Pachyglossa* (see fig. 18-1). The trio of genera—*Clasmatocolea*, *Lophocolea*, and *Pachyglossa*—are an intermeshed ensemble of taxa, each relating to the other two genera (see fig. 2).

The genus *Hepatostolonophora* should be mentioned in this discussion,

for in several respects it is involved in the *Clasmatocolea-Pachyglossa* connection. As outlined in Engel (1979b), *Hepatostolonophora* differs from *Clasmatocolea* as follows: (a) the presence of stolons; (b) the reduced, inconspicuous gynoecial bracteoles that are hardly modified from underleaves; (c) the vertically oriented, subtransverse leaves (although some facies of *H. paucistipula* have succubously oriented leaves); and (d) the dimorphic leaf cells, with the majority possessing oil-bodies, although 10-12 percent of the cells lack them.

In one way or another, one can state that all the genera discussed here are involved in a web of relationships. One ally of *Clasmatocolea*, however, forms an exception, and this is the genus *Xenocephalozia*, which seems to be connected to this complex only through kinship with *Clasmatocolea*. The deep concavity of the leaf, with the ventral portion incurved and flattened parallel to the ventral stem surface, as well as the strongly trigonous perianths with bifid lobes, remind one of *Clasmatocolea*, especially of *C. trachyopa*. However, the narrow, transverse to weak incubous leaf insertion of *Xenocephalozia* is in my mind a fundamental difference negating any real, close relationship (see notes on p. 194).

Clasmatocolea may be separated from all other members of the family by the key below.

Key to Lophocoleaceae[5]

1. Gynoecial bracts and bracteole not fused to form a tube, the perianth clearly visible, not completely enveloped by bracts 2
   2. Perianths ± strongly laterally compressed, the mouth truncate, wide, basically 2-lipped. Plants often ± brownish, often intensely so 3
      3. *Andrewsianthus*-type branching present; leaves medially to basally polystratose; flagelliform branches present; stem tissue with endophytic hyphae ..... *Evansianthus*
      3. *Andrewsianthus*-type branching absent; leaves unistratose throughout; flagelliform branches absent; stem tissue without endophytic hyphae .. *Leptoscyphus*
   2. Perianths trigonous to trigonous inflated 4
      4. Perianths all or for most part restricted to strongly abbreviated lateral- and/or ventral-intercalary branches 5
         5. Ventral margin of leaves and lateral margins of underleaves with a pouch *Tetracymbaliella*
         5. Ventral margin of leaves and lateral margins of underleaves without a pouch 6
            6. Androecia poorly differentiated, interterminal or calary on leading axes; androecial bracts much like leaves except for a small, dorsal flap or lobule and an associated small, local pocket or concavity .. *Chiloscyphus*
            6. Androecia spicate, usually on short, abbreviated lateral- or ventral-intercalary branches; androecial bracts clearly differentiated from leaves,

[5] A few portions of key adapted from Schuster (1963).

lobule large and conspicuous, the entire bract base ventricose..... *Heteroscyphus*

4. Perianth normally on more or less long branches (branches rarely abbreviated and never consistently so).....7
7. Plants stoloniferous.[6] Leaves (exc. in *H. paucistipula*) transverse to subsuccubously oriented.....8
8. Plants nearly isophyllous, the underleaves conspicuous and rigidly patent; leaves and underleaves polystratose at least at the base; female bracteoles ± similar in size to bracts.....*Pachyglossa*
8. Plants clearly anisophyllous, the underleaves highly reduced, inconspicuous, appressed to moderately spreading; leaves unistratose throughout; female bracteoles reduced, inconspicuous, hardly modified from underleaves.....*Hepatostolonophora*
7. Plants usually lacking stolons.....9
9. Leaves moderately to deeply adaxially concave.....10
10. Leaves strongly succubous, the insertion a long, strongly oblique line.....11
11. Underleaves free or connate on 1 or both sides by a few cells; leaves (exc. *C. marginata*) unistratose throughout; perianths unistratose, usually wide mouthed; plants occasionally with brown pigments, never with red.....*Clasmatocolea*
11. Underleaves distinctly and conspicuously connate on 1 side by several cells; leaves bistratose toward the base; perianth 2(-3)-stratose in median portion, abruptly contracted at the mouth; plants with brown or red-brown secondary pigments..... *Apothomanthus*
10. Leaves transverse, subsuccubous or subincubous, the insertion narrow.....12
12. Leaf margins (and abaxial leaf faces) crenulate to mamillate with domelike cell wall protuberances; leaves *Cephaloziella*-like, at most slightly concave, without an incurved ventral margin, normally lacking any trace of teeth; leaf insertion transverse to weakly succubous.....*Pigafettoa*
12. Leaf margins (and abaxial leaf faces) not crenulate to mamillate with domelike cell wall protuberances; leaves ± *Nowellia*-like, strongly concave, the ventral margin incurved and accentuating and defining a deep pocket-like concavity in ventral portion of leaf, the leaves with accessory teeth; leaf insertion transverse to weakly incubous.....*Xenocephalozia*
9. Leaves convex, rarely plane, with apices decurved or deflexed.....13
13. Leaves with lobes and marginal teeth caducous, often giving leaf apices a ragged appearance; leaf apices often with accessory teeth and laciniae.....*Leptophyllopsis*
13. Leaves entire or if lobed, then with lobes persistent; leaves with marginal teeth, if present, persistent; leaf apices never with a ragged appearance and not with accessory laciniae.....*Lophocolea*

[6] Care should be taken in search of stolons before concluding that they are absent, because *H. paucistipula* does not have stolons uniformly present on all axes.

1. Gynoecial bracts and bracteole fused to form a tube that encloses and hides the perianth..... *Conoscyphus*

VII. PHYTOGEOGRAPHY

The genus *Clasmatocolea* is among a large group of hepatic genera confined, or essentially so, to the south temperate and subantarctic regions of the world. The distribution patterns of *Clasmatocolea* species may be arranged in the categories below. Categories are provided even though species of *Clasmatocolea* do not fall within them.

TEMPERATE

Species occurring within the south temperate and sometimes subantarctic regions of the world. Species included here are regarded as temperate rather than subantarctic, because northward extension is not confined to higher altitudes (see Nontemperate, Subantarctic category below).

Pan-Temperate

Species occurring in temperate regions of South America, New Zealand, Tasmania-Australia, and South Africa.

C. vermicularis

Amphipacific Temperate

Distribution occurring in temperate parts of the South Pacific in the Southern Hemisphere, *i.e.*, temperate South America and the New Zealand sector.

C. humilis
C. notophylla

Amphiatlantic Temperate

Distribution mainly in temperate parts of the south Atlantic, *i.e.*, temperate South America and South Africa.

None

American Temperate

Species occurring within the south temperate regions of the American sector.

Fuegian.—Species restricted to Tierra del Fuego, *i.e.*, south of the Strait of Magellan.

None

Magellanian.—Species occurring in an area bounded by Cape Horn and 48° S. The northern boundary was affixed by Skottsberg (1916) to delimit the Magellanian and Valdivian regions and has been widely followed by various authors. This category includes the previous (*Fuegian*) one.

C. moniliformis

Magellanian-Valdivian.—Species essentially widespread in the South American temperate zone. They are represented in the Magellanian region and also the Valdivian region, which lies between 48° S. and 36° S. Skottsberg (1916, p. 13) places the northern boundary of the Valdivian region at 40° S., whereas Kuschel (1960) states that the zone occurs from 36° S. in the Andes, 37° S. in the coastal range, and 38° S. in the central valley. The taxa listed below are arranged according to their northernmost latitudinal range. A dagger indicates occurrence in the Falkland Islands, and an asterisk represents occurrence on the Tristan da Cunha Group.

**C. minutiretis* (41° 00′ S.)	*C. cucullistipula* (39° 16′ S.)
†*C. obvoluta* (40° 45′ S.)	*C. gayana* (37° 46′ S.)
C. puccioana (40° 07′ S.)	†*C. fulvella* (36° 50′ S.)
C. trachyopa (39° 56′ S.)	*C. navistipula* (36° 50′ S.)
C. ctenophylla (39° 52′ S.)	†*C. rigens* (33° 21′ S.)

South African Temperate

Species occurring in the Cape Region.

C. fasciculata

Australasian Temperate

Species occurring in New Zealand and/or Tasmania. A dagger indicates occurrence on New Zealand, an asterisk indicates occurrence on the New Zealand shelf islands, and a double dagger indicates occurrence on Tasmania. Species in temperate portions of Australia would ordinarily fall in this category, but the only *Clasmatocolea* taxon occurring in Australia (*C. humilis*) is amphipacific temperate, q.v.

†*C. crassiretis*	†*‡*C. strongylophylla*
‡*C. marginata*	‡*C. verrucosa*

NONTEMPERATE

Subantarctic

Species occurring on one or more subantarctic islands (as defined by Greene, 1964) of one or more sectors (e.g., American, African, or New Zealand) with northward extensions only at higher altitudes. See additional notes in Engel (1978, pp. 35-36).

None

Antarctic

Species occurring in the Antarctic Zone (as defined by Greene, 1964) with northward extensions into the subantarctic or temperate zones only at higher altitudes.

None

Malaysian Montane

Species occurring in the mountains of Malaysia.

C. tjiwideiensis

Clasmatocolea vermicularis represents the other example of northward penetration beyond temperate latitudes, but this species is widespread in austral areas, being pan-temperate plus well distributed on several subantarctic islands. Its distribution northward is strictly at higher altitudes in the Andes and higher eastern African mountains.

The exception to the strict south temperate-subantarctic range of the genus is *C. tjiwideiensis* of high-altitude Java, the only extra south temperate species. It appears that this species has been isolated for some time, for it has such features as magenta rhizoids (all other *Clasmatocolea* species having colorless rhizoids) and a unique pattern of leaf armature.

Often the areas where a species or group does not occur are just as significant or interesting as where it does occur. *Clasmatocolea* is a cool-temperate, drought-intolerant genus, and much of its local, austral distribution is explainable on this basis. The paucity of species in South Africa (two species, only one endemic) can probably be attributed to the area being both too warm and too arid for the genus. The same factors, but to a lesser degree, might explain the paucity of the genus in Australia, where *none* of the taxa confined to the Australasian temperate region (see above) occur. Only the amphipacific *C. humilis* occurs in Australia. There are no records of the genus in New Guinea at high altitudes, where one would expect the genus to occur. In fact, except for the Malaysian locality, *Clasmatocolea* does not occur north of Australia.

The distribution patterns of *Clasmatocolea* illustrate that the genus is intimately associated with the concept of continental drift and the former presence of a large southern land mass. This supercontinent, Gondwanaland, originated from the breakup of Pangaea around the middle of the Triassic (200 m. y. BP) (Dietz & Holden, 1970a, 1970b) and consisted of South America, Africa, India, Antarctica, and Australia (see fig. 3). With the juxtaposition of these continents making up Gondwana, Schuster (1972a) and Raven & Axelrod (1974) emphasize the availability of a migratory route that involved the fringes of Antarctica. Further, these authors point out that this route was available for a very long period of time. The Gondwanaland configuration shown in Figure 3 was presented in Dietz & Holden (1970a) and is quite similar to those in Schopf (1970) and Smith & Hallam (1970), the former of which is shown in Figure 4. The Schopf as well as Smith & Hallam schemes are helpful for our purposes, because the configurations show the presumed positions of Tas-

FIG. 3. Reconstruction of continental blocs at the end of the Triassic (180 m. y. BP), with a northern group of continents, Laurasia, and a southern group, Gondwana. The dotted lines indicate rift lines. (After Dietz & Holden, 1970a.)

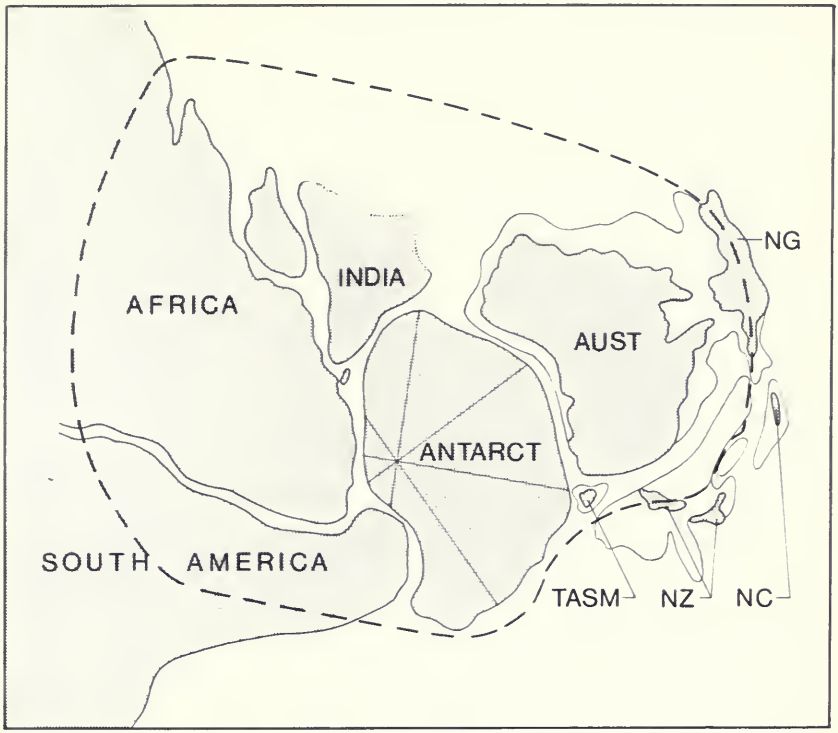


FIG. 4. Reconstruction of Permian positions of Gondwanaland continents. Tasm = Tasmania; Aust = Australia; NZ = New Zealand; NC = New Caledonia; NG = New Guinea. (After Schopf, 1970.)

mania and New Zealand. The dating of Gondwanaland differs somewhat—the Schopf model is Permian and thus earlier than the Triassic model of Dietz & Holden or the Jurassic model of Smith & Hallam. The dating of the supercontinent is less important than the possible migratory pathways available from southern South America along the fringes of Antarctica to Australia, New Zealand, and Tasmania, or, of course, the reverse. This migratory pathway is of fundamental importance in understanding the phytogeography of the far south. Returning to the Dietz & Holden models, there were two important events taking place by the end of the Jurassic or beginning of the Cretaceous (180-135 m. y. BP) (see fig. 5)—one is that there was some northward migration of the Antarctic-Australian bloc, and the other is the narrow rift (shown by the dotted line) between Africa and South America. These events continued through the Cretaceous, but at different rates, so that by the end of the Cretaceous or start of the

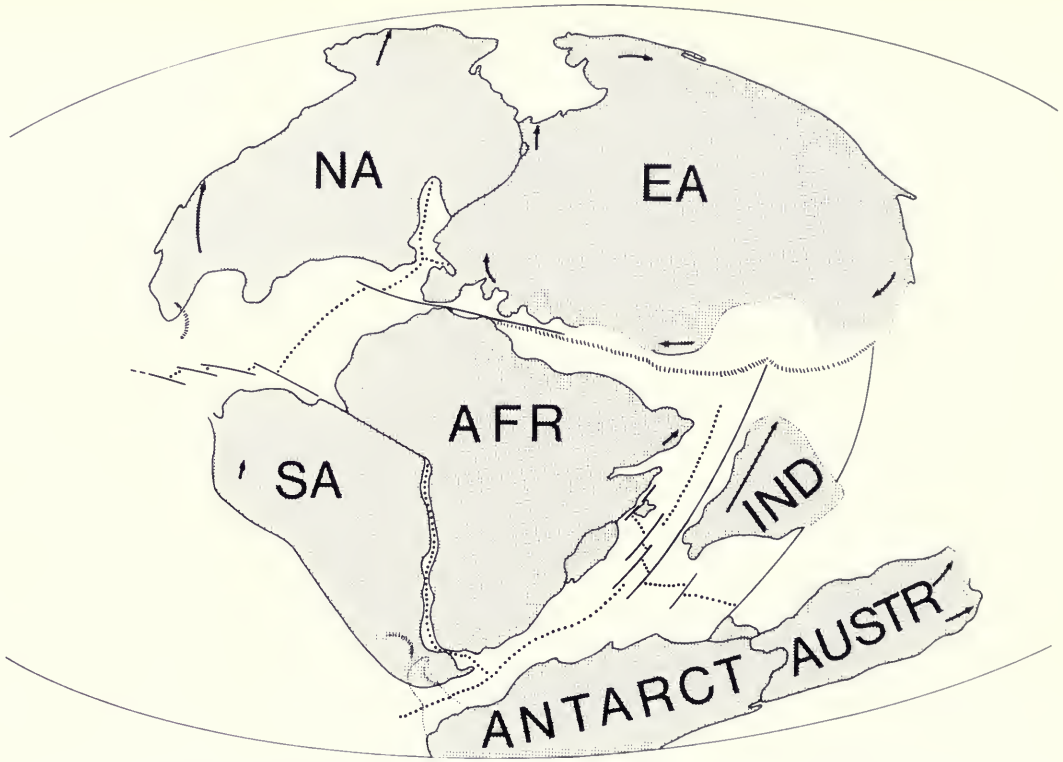


FIG. 5. Reconstruction of continental blocs at the end of the Jurassic (135 m. y. BP), showing breakup of Gondwanaland. (After Dietz & Holden, 1970a.)

Tertiary (fig. 6), Africa was isolated, but the Australian-Antarctic-South American unit did not begin to separate until some time in the Cretaceous. The separation between South America and Antarctica was narrow and presumably a phytogeographically minor one, meaning that by the early Tertiary (60-65 m. y. BP), a major austral migratory pathway still existed between southern South America and Tasmania-Australia via the Antarctic bloc. New Zealand, however, separated from Australia-Antarctica 80 m. y. BP (Raven & Axelrod, 1972, 1974).

The extant range of the most primitive groups would indicate that the genus *Clasmatocolea* originated in the southern South American sector of Gondwanaland. Of the two most primitive subgenera—Subg. *Protoclasmatocolea* and Subg. *Lacerifolia*—all species occur in the southern South American sector. The genus may have later migrated from the American sector to other southern land masses. Southern South America is also the center of distribution of the genus—of the 20 species in the genus, 15 occur in southern South America. An alternative explanation might be that the genus originated somewhere in Gondwanaland, and that the most primitive groups, or their ancestors, had a fairly wide distribution but survived only in southern South America. It is entirely plausible to think that the primitive groups survived in an area where *most* of the species are found today and that southern South America had continuing environmental conditions necessary for survival.

Clasmatocolea occurs in both forested and alpine areas, although I would not regard any species in the genus as an obligate alpine taxon. The forest-occurring species might be thought to be remnants of an early, cool-temperate flora that characterized the forested lowland areas of the Antarctic continent. Taxa that occur at higher altitudes and that are not uncommonly represented in the alpine-subalpine zone, on the other hand, might then represent remnants of a flora that characterized the more upland reaches of the Antarctic continent. In this connection, it is interesting to speculate on the history of the pan-temperate and amphipacific taxa. All species with these patterns—the pan-temperate *C. vermicularis* and the amphipacific *C. notophylla* and *C. humilis*—are not unusual in the subalpine-alpine zone in one or more sectors of their range. Perhaps, at least within the genus *Clasmatocolea*, the upland species had the greatest opportunity or capacity for dispersal over wide expanses, whereas taxa more characteristic of forests did not have this opportunity or capacity. An alternative explanation might be that the taxa presently restricted to one sector were never widely distributed or that their ancestors had a wider range but have since disappeared. In any case, species confined to

FIG. 6. Reconstruction of continental blocs at the end of the Cretaceous (65 m. y. BP) or beginning of the Tertiary. Note that the South Atlantic is a major ocean and that Australia and Antarctica remain attached and the latter close to South America. (After Dietz & Holden, 1970a.

one sector are, for the most part, forest species, with only an occasional occurrence in alpine-subalpine areas.

A comparison of *Clasmatocolea* with other hepatic genera that are endemic, or nearly so, to south temperate-subantarctic regions provides some useful information. Besides strictly south temperate-subantarctic genera, also included here are those genera containing some species that are south temperate-tropical montane in the American or Australasian regions. This northward penetration in either the Andes or high-altitude Australasia in all cases is limited and in nearly all instances occurs in only one species in the genus.

It should be mentioned that there is a rather large number of small genera endemic to a *single* south temperate-subantarctic region. These are outlined in Schuster (1969, cf. his category A-1 on p. 50) and are not discussed here. Nearly all of these genera occur in southern South America or New Zealand-Tasmania-Australia, with a minimal number in South Africa. The genera occurring in more than one south temperate area, which are listed below, are all amphipacific in distribution, whereas none are amphiatlantic or pan-temperate. There is also a group of genera that is Gondwanalandic in origin, but with more extensive penetration into tropical latitudes. These genera usually have tropical species; Schuster (1969) enumerates these groups.

In comparing *Clasmatocolea* to other endemic or near-endemic genera, only those genera occurring in more than one sector of the south temperate region are included. I have arranged the genera according to broad aspects of their ecology. The number of species in the genus is in parentheses.

A. Genera strictly alpine-subalpine
   Acrolophozia (2)
   Austrolophozia (3)
   ? *Cephalolobus* (4)
   Herzogobryum (6)
   Pachyglossa (4)
   Phyllothallia (2)

B. Genera occurring all or mostly in forests
   Archeophylla (3)
   Austrolejeunea (2)
   ? *Hyalolepidozia* (2)
   Leptophyllopsis (2)

C. Genera occurring in both alpine-subalpine and forested areas; oc-

curring at lower altitudes on both the subantarctic islands and mainland areas

Allisoniella (5)
Balantiopsis (12)
Blepharidophyllum (6)
Clasmatocolea (20)
Cryptochila (6)
Gackstroemia (7)
Lepidolaena (8)
Pseudocephalozia (6)
Hepatostolonophora (3)
Triandrophyllum (3)

Clasmatocolea, with 20 species, is the only comparatively large genus of hepatics to have a near-pure south temperate-subantarctic range. Compared to *Clasmatocolea*, all of the genera in the above list are small or relatively so. Further, *Clasmatocolea* is the only pan-temperate representative. The only instances of penetration of the genus northward beyond temperate latitudes involve strictly high altitudes.

VIII. CONSPECTUS OF TAXA

Subg. **Protoclasmatocolea** Engel, subg. nov.
1. *C. rigens* (Hook. f. & Tayl.) Engel

Subg. **Lacerifolia** Steph. *ex* Engel, subg. nov.
2. *C. obvoluta* (Hook. f. & Tayl.) Grolle
   a. var. *obvoluta*
   b. var. *cookiana* (Mass.) Engel
3. *C. trachyopa* (Hook. f. & Tayl.) Grolle

Subg. **Clasmatocolea**

Sect. **Pachyclasmatocolea** Engel, sect. nov.
4. *C. marginata* (Steph.) Grolle

Sect. **Clasmatocolea**
5. *C. humilis* (Hook. f. & Tayl.) Grolle
   a. var. *humilis*
   b. var. *suspecta* (Mass.) Engel
   c. var. *polymorpha* Engel
6. *C. fasciculata* (Nees) Grolle
7. *C. vermicularis* (Lehm.) Grolle
8. *C. gayana* (Mont.) Grolle
9. *C. ctenophylla* (Schiffn.) Grolle
10. *C. crassiretis* (Herz.) Grolle

11. *C. moniliformis* Engel
12. *C. minutiretis* Engel & Grolle

Sect. **Fulvellae** Engel, sect. nov.

13. *C. fulvella* (Hook. f. & Tayl.) Grolle

Sect. **Strongylophyllae** Engel, sect. nov.

14. *C. strongylophylla* (Hook. f. & Tayl.) Grolle
15. *C. tjiwideiensis* (Sande-Lac.) Grolle

Subg. **Metaclasmatocolea** Engel, subg. nov.

Sect. **Puccioanae** Engel, sect. nov.

16. *C. puccioana* (De Not.) Grolle

Sect. **Metaclasmatocolea**

17. *C. navistipula* (Steph.) Grolle
    a. var. *navistipula*
    b. var. *parceramosa* Engel

Subg. **Squamicalyx** Engel, subg. nov.

18. *C. notophylla* (Hook. f. & Tayl.) Grolle
19. *C. verrucosa* Engel

Subg. **Plicaticalyx** Engel, subg. nov.

20. *C. cucullistipula* (Steph.) Grolle

IX. CLASMATOCOLEA

Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15:440. 1885.

Plants prostrate to suberect, occasionally erect or subpendent, various shades of green and brown, including red-brown; main axis of smaller species less than 0.5 mm. wide, of larger species to 3 mm. wide.

Branching variable, ventral- or lateral-intercalary branches usually present (but not always together in one species); *Frullania*-type present in some taxa, absent in others; *Acromastigum*-type developed in one species; stolons absent.

Stems with cortex in 1-3 rows of cells or with cortex hardly differentiated. Rhizoids colorless or magenta, from stem near underleaf base, rarely from stem near ventral base of leaf, the tips simple or branched.

Leaves usually unistratose throughout, rarely with leaf margins 2-4-stratose and forming an elevated border, rarely with median-basal area 2-4-stratose, the leaves succubously oriented, insertion oblique, not or slightly to distinctly recurved at ventral end; leaves usually conchiform concave, occasionally moderately adaxially concave; apex undivided or 2(-3)-lobed, rarely with accessory lobes; margins entire or variously armed with teeth, laciniae or, exceptionally, accessory lobes.

Leaf cells thin to moderately thick walled, trigones large to bulging to coarse and nodular, less commonly absent, small, or medium; cuticle smooth or roughened or with coarse, hemispherical to oblong, hyaline papillae or verrucae. Oil-bodies throughout leaf, rarely absent from marginal 1-2 rows of cells, of the grape-cluster type, with the surface appearing granular or papillose; oil-bodies consistently 2 or 2-3 per cell in leaf middle.

Underleaves distinct, persistent, 0.35-6.7 × stem width, free or connate on 1 or both sides, insertion nearly always weakly to strongly arced, rarely straight; underleaves plane or convex (ventral view), sometimes cucullate, with apices undivided or bidentate to retuse to bifid to 0.7, rarely divided nearly to the base, the apex with teeth or segments usually terminating in a slime papilla; margins of the lamina entire or dentate to laciniate to 1-lobate or merely with slime papillae, the armature usually terminating in a slime papilla.

Gemmae absent; asexual reproduction rare, by regeneration from cells of leaf apex.

Plants dioecious (at least those seen); androecia terminal or intercalary on leading axes or on short, abbreviated branches, clearly differentiated from leaves; bracts (at least in basal half) strongly saccate, the distal portion usually strongly concave, the bracts sometimes with saccate portion fused toward base with opposite bract; bracts with the dorsal base dilated and forming an infolded flap or lobule; lobule large in proportion to bract size, the margin entire or dentate to laciniate or with one involute lobe, the lobule margin usually with slime papillae; bracts rarely conduplicately bilobed; antheridia solitary, rarely 2 per bract, stalk uniseriate throughout or with localized bistratose areas or 4-seriate.

Gynoecia on main axis or elongated branches or on short, abbreviated ventral- or lateral-intercalary branches; vestigial stem perigynium or coelocaule precursor sometimes present; bracts in 2-4 series, becoming progressively larger toward the perianth, those of innermost series with apices undivided to retuse or bifid, rarely trifid; margins entire or dentate to ciliate to laciniate. Bracteoles of innermost series conspicuous, considerably modified from underleaves, free, rarely connate on both sides; apices undivided or retuse to bidentate to bifid to 0.2(-0.5); lamina margins entire or dentate-laciniate-lobate. Perianth inflated, weakly to strongly trigonous to terete, particularly toward the base, the mouth wide, exceptionally contracted, 3-lobed; lobes broadly rounded, the ventral sometimes smaller and more narrowly rounded, the lobes entire or dentate to ciliate to laciniate, sometimes bifid; keels often winged.

Seta in transverse section with epidermal cells not greatly differentiated from the scattered, numerous inner cells. Capsule wall of 3-6 layers, the outer row of cells larger, equal to thickness of 1.8-3.9 of interior strata, the outer layer with thickenings on radial walls, the thickenings nodule-like to spinelike, semiannular bands present or absent; intermediate layers with thickenings on radial walls; inner layer of cells with thickenings on radial and tangential walls, semiannular bands extending from radial walls, the bands sometimes incomplete, the radial walls often with nodulose thickenings. Spores light brown or red-brown, exine with granulate grading to short vermiform ridges that have nanogranules, or the exine with narrowly conical projections having dilated tips; spores averaging 1.1-2.8 × elater diameter. Elaters bispiral.

Lectotype (*fide* Grolle, 1956): *Clasmatocolea heterostipa* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15:441. 1885.

X. Key to Taxa of Clasmatocolea

1. Leaves basically 2-3-lobed; perianth lobes bifid.....2
   2. Underleaves bifid from ca. 0.5 to usually near the base, often semiobliquely inserted; leaves usually oriented toward axis apices; opposing male bracts free;

coelocaule precursor absent; spores averaging 2.4 × elater diameter. Subg. *Protoclasmatocolea*.....*C. rigens* (p. 44)

2. Underleaves 0.12- to slightly less than 0.5-bifid; leaves strongly erect, not oriented toward axis apices; opposing male bracts fused toward base; coelocaule precursor present; spores averaging 1.1-1.4 × elater diameter. Subg. *Lacerifolia*...3
   3. Dorsal lobe acuminate; leaves with dorsal and median (if trifid) or ventral (if bifid) lobes with several opposing small to large and spinescent teeth or short cilia and often a few laciniae; underleaves free or connate on 1 side, 0.25- to slightly less than 0.5-bifid.....*C. trachyopa* (p. 60)
   3. Dorsal lobe medium- to wide-triangular; leaves with dorsal lobes entire or with 1-2 pairs of opposing teeth, the ventral lobes entire, at most with a single tooth at ventral base; underleaves nearly always connate on both sides, 0.12-0.23-bifid.....*C. obvoluta* (p. 50)

1. Leaves unlobed; perianth lobes broadly rounded, undivided.....4
   4. Underleaves with one conspicuous lobe in basal portion of underleaf that extends beyond dorsal surface of stem, the underleaves cucullate, auriculate at the base; androecia wider than sterile portion of axis, the bract lobules frequently 1-3-laciniate to lobate; perianths stoutly ovoid, the apical portion 4-5-plicate; spores 24-27(-30) μ, the exine with narrowly conical projections. Subg. *Plicaticalyx*.... *C. cucullistipula* (p. 183)
   4. Underleaf armature, if present, *not* represented by a single basal lobe extending beyond dorsal surface of stem; androecia narrower than sterile portion of axis, the bract lobules entire, dentate, or with 1 lacinium or lobe; perianths various but not stoutly ovoid (exc. *C. verrucosa*), the apical portion without plicae; spores to 24 μ.....5
      5. Underleaves connate with leaves on both sides, attachment with either ventral margin or ventral-basal portion of leaf; leaf cell lumen, except for the abbreviated thin-walled places, bounded mostly by the massive, protuberant often confluent trigones; perianth basal portion with large scales. Subg. *Squamicalyx*..6
         6. Leaf cells each with one prominant, domelike, hyaline cuticular verruca; leaves with dorsal and ventral margins irregularly dentate; underleaves reniform, 4.4-5.1 × the stem width; *Frullania*-type branching predominant *C. verrucosa* (p. 179)
         6. Leaf cells with cuticle smooth or at most roughened; leaves with margins completely entire; underleaves orbicular to oblate, 3.1-3.6 × the stem width; *Frullania*-type branching absent.....*C. notophylla* (p. 173)
      5. Underleaves free or connate on 1 side, never connate with laminal portion of leaf [or if connate on both sides (*C. tjiwideiensis*), then with leaves dentate]; leaf cell lumen bounded mostly by cell wall, the trigones consuming only fraction of boundary (exc. in *C. crassiretis*); perianth lacking scales.....7
         7. Underleaves of main axis and/or lateral-intercalary branches inconspicuous, reduced, scalelike, polymorphous, often of only a few cells. Leaves entire. Subg. *Metaclasmatocolea*.....8
            8. Underleaves of *main axis* well developed; lateral-intercalary branches copiously produced, of limited growth, usually abbreviated; main axis underleaves with segments of similar size and shape; male bracts not conduplicately bilobed; plants light brown-sienna; main axes 560-910 μ wide. Sect. *Puccioanae*.....*C. puccioana* (p. 157)
            8. Underleaves of *main axis* reduced; lateral-intercalary branches usually

of unlimited growth; main axis underleaves frequently with asymmetric segments; male bracts conduplicately bilobed; plants whitish-light green; main axes 455-595 μ wide. Sect. *Metaclasmatocolea*.....
C. navistipula (p. 165)

7. Underleaves of main axis and branches conspicuous, not reduced or if inconspicuous and reduced (*C. minutiretis*), then leaves with several teeth. Subg. *Clasmatocolea*.....9
   9. Leaf and sometimes underleaf margins conspicuously swollen, the elevated border 2-4-stratose; leaf lamina 2-4-stratose in median-basal area; antheridial stalks 4-seriate. Sect. *Pachyclasmatocolea*.....
   C. marginata (p. 69)
   9. Leaf and underleaf margins not swollen or elevated, unistratose; leaf lamina unistratose throughout; antheridial stalks 1-2-seriate.....10
      10. Leaf cuticle with coarse, hemispherical, hyaline papillae. Sect. *Strongylophyllae*.....11
         11. Underleaves plane to weakly convex (ventral view), 1-2 × stem width; leaves entire; rhizoids colorless.....
         C. strongylophylla (p. 147)
         11. Underleaves deeply concave to ± cupulate (ventral view), 3.3-4 × stem width; leaves with ventral margin 1-3-dentate toward the base; rhizoids magenta.....*C. tjiwideiensis* (p. 154)
      10. Leaf cuticle smooth or slightly roughened.....12
         12. Intercalary branches appearing quite different from main axis, the branches vermiform and submoniliform, narrower in width than main axis, commonly copiously produced and short, abbreviated, with underleaves more closely imbricate than in main axis. Leaves of main axis sinuate and incurved; intercalary branch underleaves large, orbicular, distinctly cupulate, appearing inflated. Sect. *Fulvellae*.....*C. fulvella* (p. 139)
         12. Intercalary branches not vermiform or submoniliform (exc. *C. moniliformis*), usually of same width as the main axis, often very long, with underleaves not conspicuously more closely imbricate than in main axis (exc. in some plants of *C. humilis* var. *suspecta*, q. v.). Sect. *Clasmatocolea*.....13
            13. Leaves with 17-32 regularly spaced 1-2(-4)-celled teeth subequal in size.....*C. ctenophylla* (p. 119)
            13. Leaves entire or if armed, then with 1-10 teeth or laciniae, armature irregularly spaced, commonly several- or many-celled, and only rarely with teeth consistently 1-2-celled..14
               14. Underleaves consistently narrower than stem.....15
                  15. Leaf margins entire; leaf cell trigones usually absent to small, occasionally medium; terminal branching occasional; opposing male bracts free. Perianths inflated, clavate-campanulate, distinctly or obscurely trigonous at the base, obscurely so toward the apex, mouth truncate, *wide*, the three lobes rotund, entire, occasionally emarginate.....
                  C. vermicularis (p. 96)
                  15. Leaf margins with several, often incurved, teeth; leaf cell trigones large to knotlike; terminal branching

absent; opposing male bracts fused toward base... *C. minutiretis* (p. 133)

14. Underleaves (0.9-)1.0-4.3 × stem width.....16
    16. Underleaves with an associated, raised, flat, disciform rhizoid initial field; axis apices and intercalary portions very commonly enlarged; perianth keels with wings large and conspicuous, occasionally sinuate, the perianth mouth rather densely denticulate with teeth predominantly uniseriate..... *C. gayana* (p. 112)
    16. Underleaves without an associated rhizoid field; axes of approximately same width throughout; perianth keel wings, if present, never large and conspicuous, never sinuate, perianth mouth entire, dentate or laciniate, never consistently denticulate with teeth predominantly uniseriate.....17
        17. Underleaf lamina margins usually with 1 large often apiculate lacinium, margins otherwise entire or sparingly dentate to ciliate to laciniate; perianths restricted to short ventral-intercalary branches, the perianths slightly narrowing toward mouth. Branches usually with first 1-2 pairs of leaves bifid.....*C. fasciculata* (p. 91)
        17. Underleaf lamina margins *with* 1 tooth or lobe or entire, *without* 1 large lacinium; perianth position variable, on main axis or on short to long intercalary branches, but never restricted to short ventral-intercalary branches, the perianth with sides straight or gradually expanding toward the mouth.....18
            18. Underleaves to 1.3 × stem width, plane and not convex (ventral view); stems 5-6 cells high; plants often corticolous. Perianth terete, the ventral side not infolded..... *C. crassiretis* (p. 124)
            18. Underleaves to 6.7 × stem width, slightly to deeply convex to cucullate (ventral view); stems 6-14 cells high; plants terricolous, saxicolous, or on rotted logs.....19
                19. Axes not moniliform, to 1.8 mm. wide, larger; branching with lateral-intercalary type common, *Frullania*-type occasional; leaf cells thin walled; leaf insertion slightly to distinctly recurved at ventral end.....*C. humilis* (p. 74)
                19. Axes moniliform, to 1.4 mm. wide, smaller; branching with lateral-intercalary type absent, *Frullania*-type very rare, ventral-intercalary type common; leaf cells distinctly thick walled; leaf

insertion not recurved at ventral end. Underleaves cucullate, inflated, with apices closely appressed to the stem...
C. moniliformis (p. 128)

Subg. **PROTOCLASMATOCOLEA** Engel, subg. nov.

Folia caulina bifida ad 0.15-0.3, plerumque longitudo magis quam latitudine et disposita versus axis apicem; cellulae foliorum trigonae minutae ad medias; amphigastria caulina saepe semioblique inserta, bifida e 0.5 ad plerumque prope basin; perianthiarum lobi bifidi.

Type species: *Clasmatocolea rigens* (Hook. f. & Tayl.) Engel.

Leaves bifid to 0.15-0.3, usually longer than wide and oriented toward axis apex; trigones minute to medium; underleaves often semiobliquely inserted, bifid from 0.5 to usually near the base; perianth lobes bifid.

Distribution.—Falkland Is. and Dependencies, southern South America.

Clasmatocolea rigens (Hook. f. & Tayl.) Engel. Figures 7-9, Plates 1, 2.

Jungermannia rigens Hook. f. & Tayl. London J. Bot. 3:461. 1844. *Cephalozia rigens* (Hook. f. & Tayl.) Trev. Mem. Ist. Lomb. Sci. Lett. III. 4:417. 1877. *Lophocolea rigens* (Hook. f. & Tayl.) Evans, Bull. Torrey Bot. Club 25:423. 1898. *Clasmatocolea rigens* (Hook. f. & Tayl.) Engel, J. Hattori Bot. Lab. 36:156. 1973. Original material: Falkland Is., *Hooker* (BM!).

Lophocolea koeppensis Gott. Ergebn. Deutsch. Polar-Exped. 2 (16):453. *pl. 2, f. 4-9.* 1890, *syn. fide* Engel (1973a). *Clasmatocolea koeppensis* (Gott.) Grolle, Rev. Bryol. Lichénol. 29:72. 1960. Lectotype (*fide* Grolle, 1972b): South Georgia, Köppenberg, 10 February 1883, *Will 35* (M!).

Lophocolea debilis Steph. Kongl. Svenska Vetenskapsakad. Handl. 46 (9):42. *f. 19 a-c.* 1911, *syn. fide* Engel (1973a). Lectotype (*fide* Engel, 1973a): Chile, Prov. Magallanes, S. Skyring, Pta. Eulogio, 22 April 1908, *Halle & Skottsberg 196* (UPS!; isolectotype: G!).

Lophocolea stephanii Herz. Hedwigia 64:5. *f. 2.* 1923, *syn. nov., non L. stephanii* Schiffn. Hep. Fl. Buitenzorg p. 181. 1900. Holotype: Chile, Prov. Valdivia, Valdivia, December 1911, *Herzog* (JE!).

Lophocolea olens Herz. Arch. Esc. Farm. Fac. Ci. Med. Cordoba 7:16. *f. 5.* 1938, *syn. nov.* Lectotype (*nov.*): Chile, Prov. Cautín, Pucón, "Halbinsel," *Hosseus 140* (JE!).

Plants *rather fragile (especially small facies)*, prostrate, but axes often sharply curved dorsally, *often in dense, thick mats, usually pale green*, occasionally light brown, nitid when dry; *axes to 2 mm. wide with leaves spread, small facies 200-460 μ wide.*

Branches mostly of Frullania*-type, often slender and copiously produced*, associated

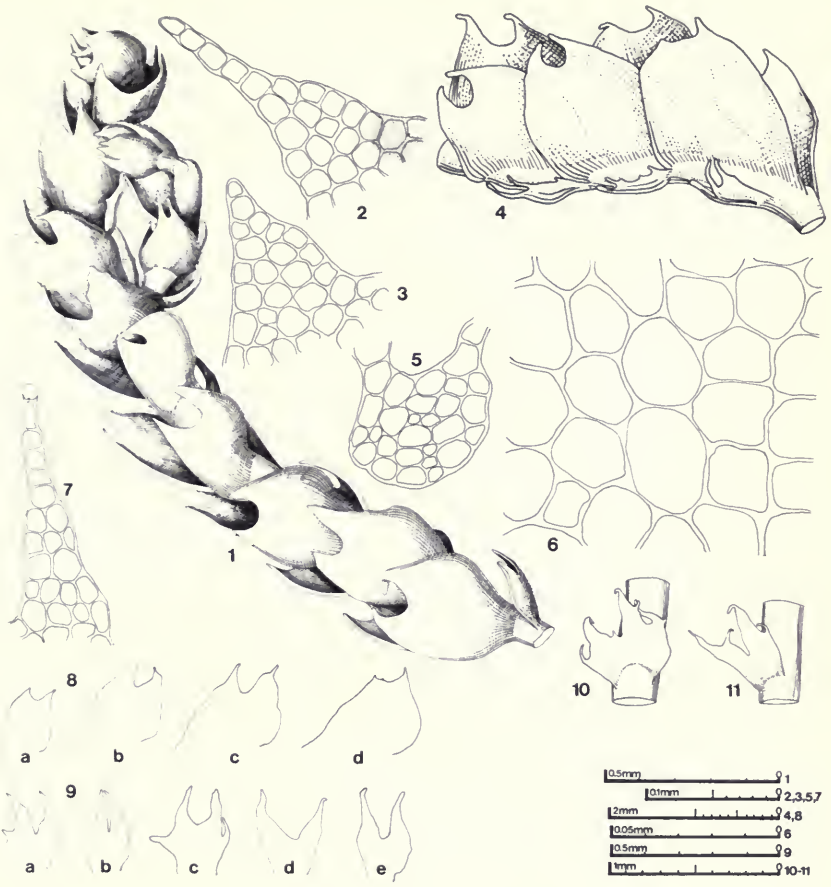


FIG. 7. *Clasmatocolea rigens* (Hook. f. & Tayl.) Engel. **1,** Portion of main axis, small facies of species, lateral view. **2,** Leaf lobe, apical portion, roughened cuticle shown at lower right. **3,** Leaf lobe. **4,** Portion of main axis, lateral view. **5,** Stem, cross section. **6,** Median leaf cells. **7,** Underleaf segment, the tip cell a partially collapsed slime papilla. **8,** Leaves. **9,** Underleaves. **10, 11,** Underleaves, note oblique insertion. Figures 1, 3, 5-8a-b, d-e, from type of *C. rigens*, *Hooker*, Falkland Is.; figures 2, 8f, from *Engel 1906*, Chile, Prov. Magallanes, E. of Mina Loreto; figure 4, from *Engel 1987*, Chile, Prov. Magallanes, 8 km. W. of Punta Arenas; figure 8c, from *Hatcher 4-13*, Chile, Prov. Magallanes, near Fuerte Bulnes; figures 10, 11, from *Engel 2008*, Chile, Prov. Magallanes, B. Camden.

half leaf usually undivided (but occasionally bifid), ± triangular-ovate, apiculate, and with margins often sinuous; *lateral-intercalary branches fairly common; ventral-intercalary branches rare;* intercalary branches occasionally short, reduced, and copiously produced.

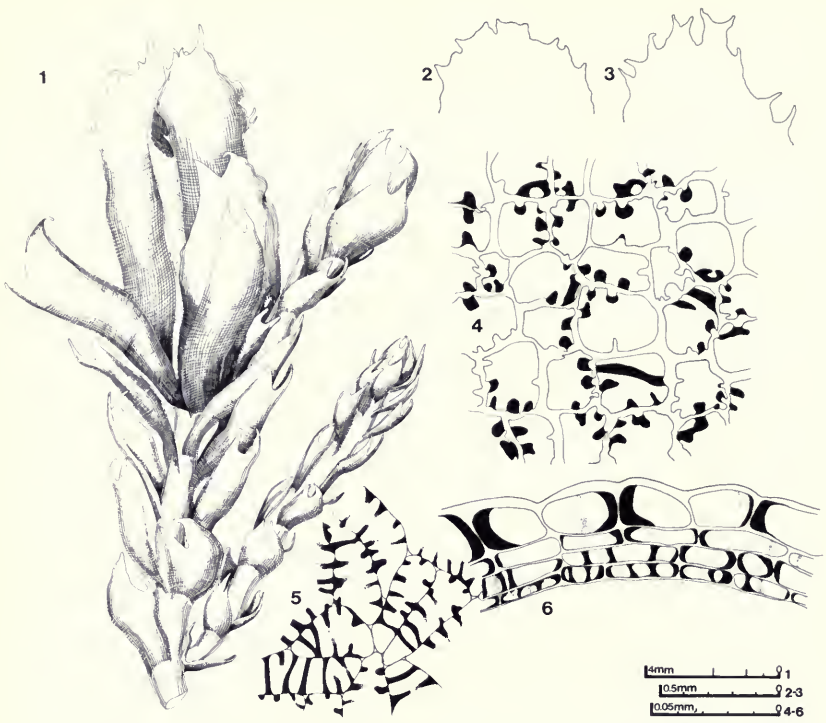


FIG. 8. *Clasmatocolea rigens* (Hook. f. & Tayl.) Engel. **1,** Axis with perianth. **2, 3,** Perianth lobes. **4,** Outer capsule wall cells to symbolize pigmented (darkened) and hyaline (unshaded) thickenings, note few semiannular bands. **5,** Capsule wall, cross section. **6,** Inner capsule wall cells. Figures 1, 2, from *Engel 2641*, Falkland Is., Mt. Usborne; figures 3, 5, from *Engel 1827*, Chile, Prov. Magallanes, Pta. Santa Ana; figures 4, 6, from *Engel 1815*, Chile, Prov. Magallanes, Pta. Santa Ana.

Stems 5-8 cells high, cortex in a single row of cells slightly smaller than, the same size as, or slightly larger than the medullary cells, exposed wall thin or moderately thickened, the cortex otherwise thin walled. Rhizoids in fascicles from stem near underleaf base.

Leaves usually longer than wide (wide ovate leaves commonly wider than long), *oriented toward axis apex and thus with dorsal margin longer than the ventral*, the insertion distinctly recurved at ventral end; *leaves erect*, (distant-) loosely imbricate, adaxially concave (a few convex leaves sporadically present, particularly on robust plants), *oblong to medium-wide ovate; leaves bifid to 0.15-0.30, the lobes medium-wide triangular and usually apiculate, often incurved*, often clawlike, the sinus narrowly-broadly rounded to lunate, occasionally triangular; margins entire or occasionally 1-dentate towards the apex, rarely 1-laciniate-lobate; *dorsal margin often more broadly rounded than the ventral*, often sinuous, commonly long decurrent; ventral margin often subauriculate at the base.

Leaf cells *thin-walled, trigones minute to medium;* median leaf cells 14-34 μ wide, (13-)18-38 μ long; cuticle smooth to roughened and appearing finely granular.

FIG. 9. *Clasmatocolea rigens* (Hook. f. & Tayl.) Engel.

Underleaves *usually slightly wider than stem, often obliquely inserted*, moderately to distinctly spreading, remote to contiguous, *bifid from ca. 0.5 to usually near the base; segments curved dorsally*, particularly at the apices, *the segments lanceolate-subulate, occasionally medium-triangular, often apiculate*, terminating in a slime papilla, the segment margins entire (-1-2-dentate-ciliate); *margins of the lamina entire or usually 1-*(to rarely 3) *dentate-laciniate-subulate*, the armature terminating in a slime papilla.

Plants dioecious; androecia terminal or intercalary on main axis, *Frullania*-type, or lateral-intercalary branches; bracts erect and oriented toward axis apex as in leaves, strongly saccate, apical portion slightly spreading but with lobes incurved, the apices often appressed to bract immediately above (in small plants); lobule margin with several slime papillae *and* often few-celled teeth terminating in slime papillae, or with 1 lacinium, or 1 large, acute or rounded involute lobe; antheridia solitary, rarely 2 per bract, stalk uniseriate throughout, very rarely with a localized bistratose area.

Gynoecia on main axis, rather long *Frullania*-type or lateral-intercalary branches

and subfloral innovations; subfloral innovations nearly always present, originating from below gynoecium, below perianth or from inside perianth; bracts in 3-4 series; those of innermost series oblong-ovate; *apices bifid* and with lobes incurved; margins entire or few dentate-ciliate-laciniate. Bracteoles of innermost series free from bracts, *0.2-0.5-bifid;* lamina margins slightly to distinctly recurved, entire-few dentate-laciniate. *Perianths often produced, strongly trigonous, elongate-subrectangular to oblong* or occasionally ± campanulate, *slightly expanding to slightly narrowing toward mouth,* the mouth closed by slightly incurved lobes or in ± campanulate-shaped perianths by infolding of ventral lobe; lobes rounded, *bifid,* sparingly to *usually densely dentate-ciliate-laciniate, very rarely subentire;* keel wings common, of a few cells high, occasionally dentate.

Seta not studied. Capsule valves 530-950 μ long, 41-53 μ thick, of 4-6 layers, outer row of cells about equal to thickness of innermost 3 strata; outer layer with vinaceous or colorless, nodule-like or ± spinelike thickenings that are often feebly tangentially dilated, a very few semiannular bands occasionally present; exposed wall thickened; outermost intermediate layer of cells thicker than inner layer, the intermediate layers with thickenings feebly extending onto tangential walls; inner layer of cells with yellow- to red-brown, semiannular bands, the bands often incomplete, often forked, the radial walls with nodulose thickenings often present.

Spores 14-18 μ, red-brown, exine with the light microscope appearing minutely punctate, but under the SEM with granulate to short, abbreviated vermiform projections that have nanogranules; spores averaging 2.4 × elater diameter. Elaters 6-7 μ wide, spiraled to tips, walls light brown.

Variation.—The original material of *Jungermannia rigens* represents a not infrequently occurring very small facies of the species. This facies superficially resembles the genus *Cephalozia,* which likely accounts for its transfer to that genus by Trevisan de Saint-Léon (1877). The underleaves of this facies have margins entire or with a few small teeth and are not lacinate-subulate as is common in larger, more robust plants. Because this facies is part of a continuum with medium and larger individuals with increasingly larger underleaf armature, I do not recognize it taxonomically.

Differentiation.—The combination of bifid leaves that are usually longer than wide and oriented toward axis apices (and thus with dorsal margins considerably longer than the ventral) and the medium-wide triangular, apiculate leaf lobes will serve to separate this species from all others of the genus. Further, in no other species are the underleaves bifid nearly to the base; underleaves in other *Clasmatocolea* taxa are, for the most part, undivided or bifid to at most 0.5.

Larger plants of *C. rigens* resemble plants of *Lophocolea lenta* (Hook. f. & Tayl.) G. L. & N., but the former may be immediately distinguished by the possession of (a) at least some adaxially concave leaves on a given axis; (b) underleaves often obliquely inserted; and (c) dioecious inflorescences. *Lophocolea lenta,* on the other hand, has (a) convex leaves; (b)

underleaves consistently transversely inserted; and (c) monoecious inflorescences.

Notes.—1. In one specimen (*Engel 1815*), two mature sporophytes were observed arising from a single inflorescence. According to Schuster (1966), this phenomenon exists in the primitive orders Calobryales and Monocleales, but is of only isolated occurrence in other groups.

2. *Lophocolea subaromatica* Herz. (Arch. Esc. Farm. Fac. Ci. Med. Cordoba 7:15. 1938) described from Pucón (Chile, Prov. Cautín) may belong here; I have not seen type material of this species.

Ecology.—In southern South America, seemingly characteristic of deciduous forests and boundaries between deciduous and evergreen *Nothofagus* forests. Rare in evergreen forest regions and then only in the drier portions. It is absent, for example, in the wet, western part of Tierra del Fuego as well as the wet *western* Patagonian Channels of Prov. Magallanes. In the Valdivian region on bark or over rocks in *Nothofagus* forests or mixed *Nothofagus pumilio-Araucaria* forests. On the South Sandwich Islands within the main crater of Bellinghausen Island, where around but away from fumaroles, and on boulders moistened, but probably not warmed, by steam (130-200 m.). Also on the slopes of the main cones, but again, away from fumaroles (75-80 m.).

Phytogeography.—South Sandwich Is. (75-200 m.); South Georgia; Falkland Is. (335-700 m.); Tierra del Fuego (sea level-300 m.; vicinity of Ushuaia and R. Azopardo); southern Patagonian Channels (Brunswick Pen., S. Skyring, Pta. Eulogia); Valdivian region (730-1,450 m.; West Patagonia from 45° 25′ S. to 38° 39′ S., Andean Patagonia at 43° 30′ S.); Prov. Santiago (see fig. 9).

Specimens seen.—**SOUTH SANDWICH IS.:** Bellinghausen I., 75-130 m., *Holdgate 421A*, *430A*, *816* as *C. koeppensis* (hb. Grolle); ibid., 75-200 m., *Holdgate 431A* — c. ♂, *479A* — c. ♂, *811*, *825* — c. ♂ as *C. koeppensis* (JE). **SOUTH GEORGIA:** Köppenberg, *Will 37* as *C. koeppensis* (M). **FALKLAND IS.** (selected). **EAST FALKLANDS:** Mt. Usborne Region, ridge between Mt. Usbornes 1 & 2, 685 m., *Engel 2538B* — c. ♂ (MSC). **WEST FALKLANDS:** Mt. Adam, E. side of summit ridge, 670-700 m., *Engel 3021* — c. ♂ (MSC). **ARGENTINA.** TERR. TIERRA DEL FUEGO: Lapataia, *Hatcher s.n.* — c. ♂ (FH); W. side of B. Lapataia, *Crow 1507* — c. per., *1509*, *1518* — c. per. (MSC); N. side of L. Roca, *Crow 1485* — c. ♂ (MSC); Ushuaia, *Dusén 287* as *Lophocolea latissima* (S); ibid., *Dusén 303* as *Lophocolea irregularis* (G — c. per., NY); ibid., Baliza, near sea level, *Roivainen 1206*, *1206b* — c. per. (F, H); Ushuaia, R. Olivia, near sea level, *Roivainen 1066* (F, H); ibid., *Roivainen*

1076b, *1080b*, *1082*, *1089b* (H); C. Garibaldi, 300 m., *Roivainen 747b* — c. per. (H); I. Observatorio, *Hässel de Menéndez 3919* (BA, F). **CHILE.** PROV. MAGALLANES: R. Azopardo, 300 m., *Halle & Skottsberg 219* as syntype of *Lophocolea monoica* (UPS); Brunswick Pen. (cf. Engel, 1978). PROV. AISÉN: R. Aisén, *Dusén s.n.* as *Lophocolea lenta* (BM); Puerto Aisén, *Schwabe 45/b p.p.* as *Lophocolea subaromatica* (JE); Valle Frias, *Skottsberg 209* as *Lophocolea humifusa* (UPS). PROV. VALDIVIA: V. Shoshuenco, *Ruthsatz s.n.* — c. ♂ (JE); SW slope of V. Quetrupillán, 1,450 m., *Engel 11156* (F). PROV. CAUTÍN: L. Quilleihue, 10.7 km. by road E. of Puesco, ca. 7 km. by road W. of Chile-Argentina boundary, 1,050 m., *Engel 11313* (F); Termas de Palguín, along R. Palguín, 730 m., *Engel 11222* (F); Parque Nac. Villarrica, N. slope of V. Villarrica, 1,150 m., *Engel 11180*, *11190* (F); Pucón, "Halbinsel," *Hosseus 363A* as syntype of *L. olens* — c. per. + ♂ (JE); V. Llaima, *Ruthsatz s.n.* (JE); Parque Nac. Conguillo, 1,050-1,120 m., *Mahu 10686* — c. per., *10695*, *10723*, *10732*, *10794*, *10822* (hb. Mahu). PROV. MALLECO/PROV. ARAUCO: Cord. Nahuelbuta, Parque Nac. Nahuelbuta, 44 km. W. of Angol, 1,300 m., *Engel 12630* (F). PROV. SANTIAGO: C. Manquehue, Q. Agua del Palo, 940 m., *Mahu 10592* — c. sporo. (F). **ARGENTINA.** PROV. CHUBUT: A. Carbon, *Halle 219* as syntype of *Lophocolea monoica* (UPS).

Subg. **LACERIFOLIA** Steph. *ex* Engel, subg. nov.

(Subg. *Lacerifoliae* Steph. Bull. Herb. Boissier 6 (7):538. 1906 [= Spec. Hep. 3:52], nom. nud.)

Folia caulina 2-3-lobis, apice ad 0.75 diviso; amphigastria caulina 0.12-0.5-bifida; oppositae ♂ bracteae connatae versus basin; praecursor coelocaulis praesens; perianthii lobae bifidae.

Type species: *Clasmatocolea trachyopa* (Hook. f. & Tayl.) Grolle.

Leaves 2-3-lobed, divided to 0.75; underleaves 0.12-0.5-bifid; opposing ♂ bracts fused toward base; coelocaule precursor present; perianth lobes bifid.

Distribution.—Southern South America and Falkland Is.

Clasmatocolea obvoluta (Hook. f. & Tayl.) Grolle. Figures 10-13, Plates 3, 4.

For synonymy see under varieties.

Plants *soft*, prostrate, mixed with other bryophytes, occasionally in pure mats, grey-green to pale brown to brown, sometimes a rich orange-brown with age; *axes to 1.5 mm. wide.*

Branches sparing to frequent, of *lateral-intercalary and* Frullania *types* (collections varying in predominance of each); *ventral-intercalary type not seen.*

Stems 9-18 cells high, cortex in 1-2(-3) rows of slightly to moderately thick-walled

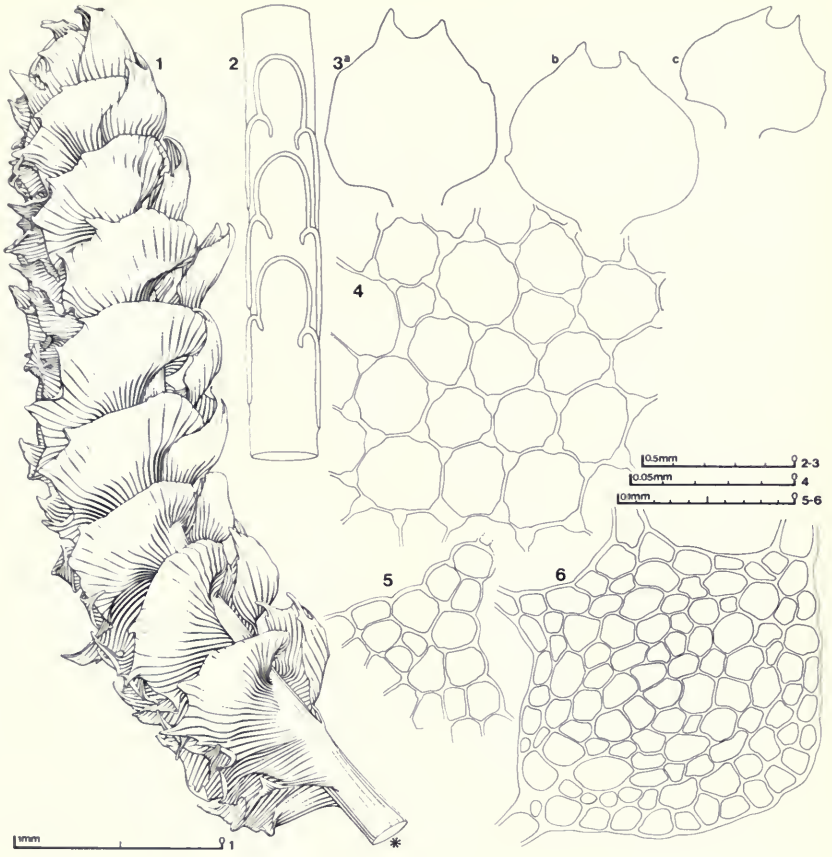


FIG. 10. *Clasmatocolea obvoluta* (Hook. f. & Tayl.) Grolle. **1,** Portion of main axis, lateral view. **2,** Main axis, ventral view showing underleaf and leaf insertion. **3a-c,** Underleaves. **4,** Median leaf cells. **5,** Underleaf segment. **6,** Stem, cross section. Figures 1, 3a-b, 4-6, from lectotype of *C. obvoluta*, *Davis*, Chile, Prov. Magallanes, Cta. San Martin; figure 2, from *Engel 4386A*, Chile, Prov. Aisén, F. Témpano; figure 3c, from *Engel 4381*, Chile, Prov. Aisén, F. Témpano.

cells slightly to distinctly smaller than or ca. equal to size of medullary cells; medullary cell walls thin; endophytic hyphae absent. Rhizoids in fascicles from stem near underleaf base.

Leaves with insertion distinctly recurved at ventral end; leaves strongly erect, with *dorsal lobes often connivent dorsally*, leaves loosely to densely imbricate, conchiform concave, *obscurely to distinctly reniform*, occasionally very wide-ovate; *leaves 0.15-0.50-bifid*, **dorsal lobe** variable in size, *medium- to wide-triangular, usually apiculate, plane or with margins reflexed lending lobe slightly to distinctly canaliculate*, rarely with margins connivent toward base and then lobe here locally tubiform, the *lobe entire or with 1-2*

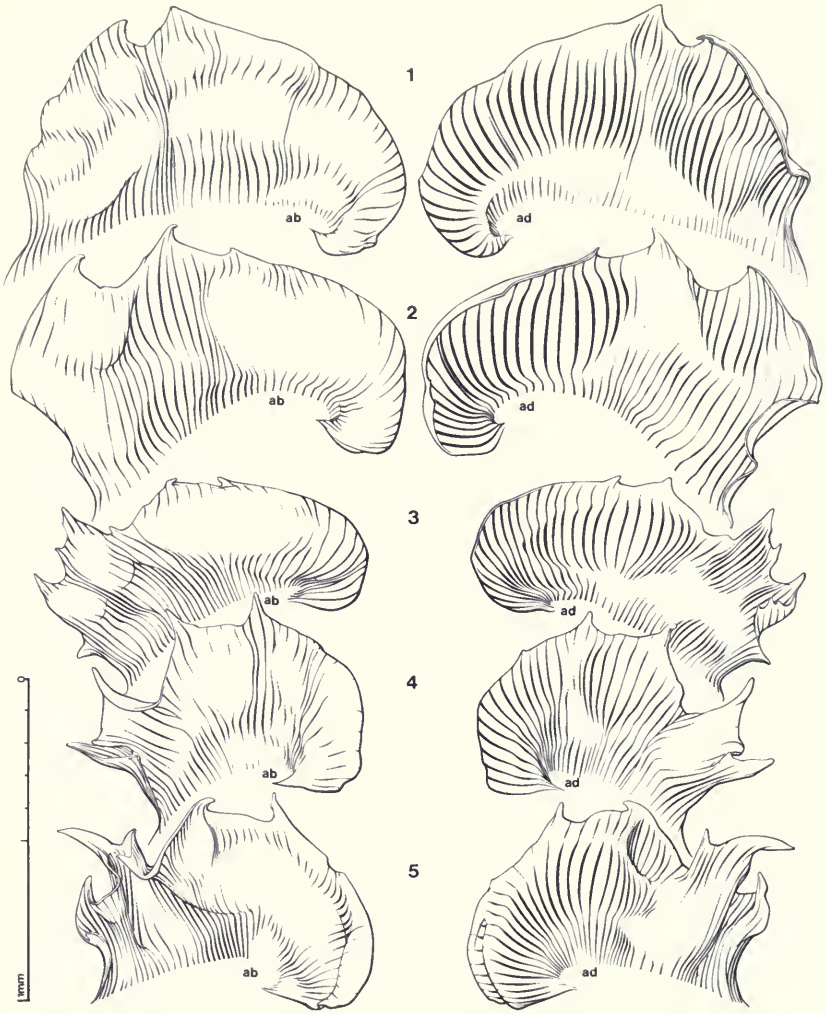


FIG. 11. *Clasmatocolea obvoluta* (Hook. f. & Tayl.) Grolle. **1-5,** Leaves, illustrating trend in apical and marginal characters. Figure 1, from lectotype of *Lophocolea cookiana*, *Spegazzini 14*, Argentina, Terr. Tierra del Fuego, Pto. Cook; figure 2, from *Engel 5581A*, Chile, Prov. Magallanes, Pto. Bueno; figure 3, from *Engel 4381*, Chile, Prov. Aisén, F. Témpano; figures 4, 5, from lectotype of *C. obvoluta*, *Davis*, Chile, Prov. Magallanes, Cta. San Martin.

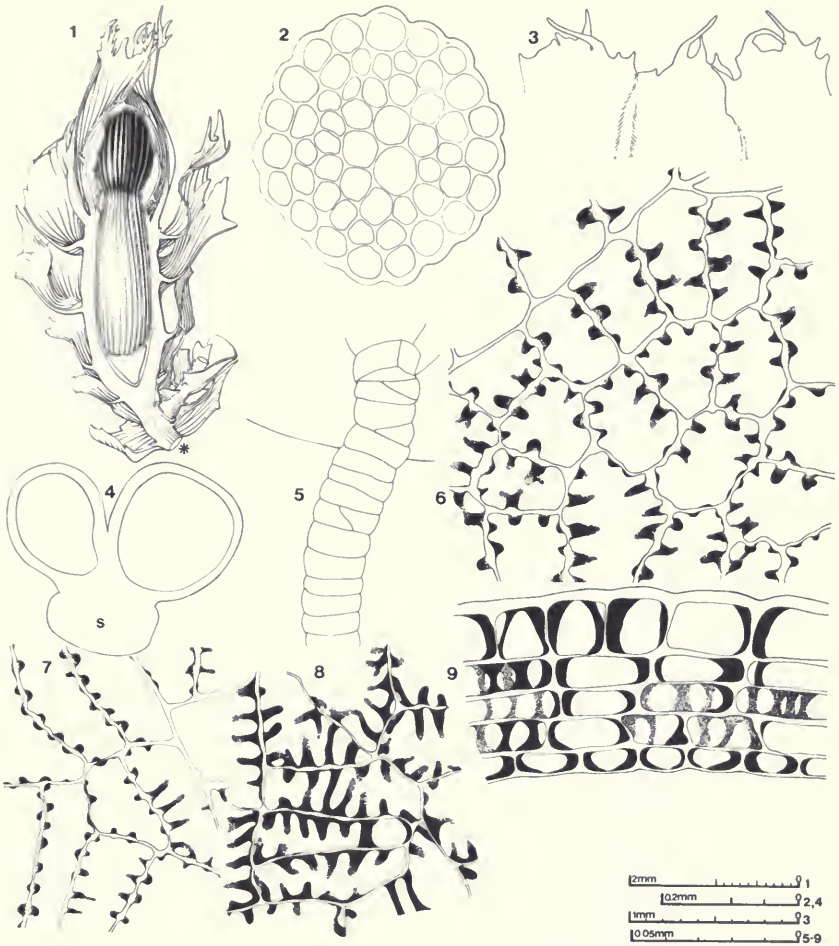


FIG. 12. *Clasmatocolea obvoluta* (Hook. f. & Tayl.) Grolle. **1,** Longitudinal section through sporophyte-bearing plant, showing axial proliferation of tissue; note position of bracts and unfertilized archegonia. **2,** Seta, cross section. **3,** Perianth, ventral lobe in middle. **4,** Opposing antheridial bracts with stem(s), cross section. **5,** Antheridial stalk. **6, 7,** Outer capsule wall cells. **8,** Inner capsule wall cells. **9,** Capsule wall, cross section. Figures 1, 8, from *Engel 4574A*, Chile, Prov. Magallanes, Pto. Edén; figures 2, 3, from *Engel 5339*, Chile, Prov. Magallanes, B. Wide; figure 4, from *Engel 4277*, Chile, Prov. Aisén, Pto. Island; figure 5, from *Engel 5890*, Chile. Prov. Magallanes, Pto. Charruca; figures 6, 7, 9, from *Engel 6034*, Chile, Prov. Magallanes, Pto. Gallant.

40°
42°
44°
46°
48°
50°
52°
54°
56°

pairs of commonly opposite teeth, the dorsal-basal portion of dorsal lobe or dorsal margin immediately proximal to lobe entire or with a tooth or small canaliculate lobe; **ventral lobe** variable in size, *very wide-triangular, occasionally medium-triangular*, apiculate, *plane, entire or with a single conspicuous tooth near base of ventral margin*, the lobe occasionally short and poorly developed; *sinus in antical 0.25-0.45 of leaf*, the tissue at sinus base plane or reflexed, often toothed; *dorsal margin* of leaf *straight*, plane or reflexed in distal portion, plane in proximal portion, not to long decurrent, entire or with 1-2 straight or reflexed teeth or laciniae in distal portion; *ventral margin broadly rounded to subauriculate*, with *basal portion enlarged, extending ventrally beyond stem and closely approaching or in contact with moderately spreading underleaves*, occasionally in contact with ventral margin of opposite leaf, the ventral margin entire or with a few small teeth.

Leaf cells thin walled, trigones medium to large and bulging to occasionally coarse and nodular; median leaf cells 19-42 μ wide, (22-)24-50(-54) μ long; cuticle smooth or slightly roughened and appearing finely granular. Oil-bodies throughout leaf, occupying small fraction of cell lumen, hyaline and glistening to tannish to "dirty white," of grape-cluster type, with numerous, very small, barely protruding globules, the oil-body surface appearing papillose; oil-bodies variable: subglobose to ovoid to elliptic to fusiform to crescentic in shape, 2-3(-4) of leaf middle, 2-4 of leaf apex, 2-5(-8) of leaf base, those of leaf middle 4-5 μ wide, (5-)6-12 μ long; oil-bodies throughout underleaf, of about the same size as those of leaf middle.

Underleaves *3-4.3* $\times$ *stem width, connate on both sides*, rarely connate on 1 side in axes with very loosely imbricate leaves, moderately spreading, approximate to loosely imbricate, *moderately convex* (ventral view), moderately to very *wide-ovate to suborbicular* (and slightly wider than long) *to subcordate;* underleaves *bifid to 0.12-0.23*, the segments terminating in a small slime papilla, the segment margins entire; margins of the lamina with 1 slime papilla or 1-2(-3) small teeth terminating in a small slime papilla, margins occasionally entire.

Plants dioecious; androecia terminal or intercalary on main axis, or short to long lateral-intercalary or *Frullania*-type branches; bracts with basal portion strongly saccate, the *saccate portion fused toward base with opposite bract;* bracts armed at apex and upper portion of dorsal margin with 2-3 sharp teeth, or bracts armed with 2 small, sharp lobes and a tooth on ventral margin near ventral lobe, the ventral margin otherwise entire; lobule margin with an inrolled rounded lobe, the lobe entire or with a few small teeth and/or slime papillae, occasionally with several low, rounded projections; antheridia solitary, stalk uniseriate throughout or uniseriate and with scattered locally biseriate areas.

Gynoecia on main axis or rather short to long lateral-intercalary or *Frullania*-type branches; subfloral innovations absent or from below bracts of first, second, or innermost series, or bracteole of second series, the innovation may, in turn, produce a perianth; *coelocaule precursor present;* bracts and bracteoles in 3 series, *inserted on coelocaule precursor;* **bracts** of innermost series moderately convex to moderately concave, elliptic to ovate, asymmetric and with dorsal margin more rounded than the ventral, or symmetric; apex often rather narrowed, very short-bifid or divided to 0.25;

Opposite:

FIG. 13. *Clasmatocolea obvoluta* (Hook. f. & Tayl.) Grolle. ● = var. *obvoluta*; ○ = var. *cookiana*; ◐ = both var. *obvoluta* and var. *cookiana*.

lamina margins with a few small to large teeth. **Bracteoles** of innermost series subequal to bracts in size, free from bracts, concave (ventral view), ovate to elliptic; apex rather narrow, very short bifid; lamina margins slightly to distinctly reflexed, entire or with a few small to large teeth. **Perianth** *strongly trigonous*, narrowly elliptic to narrowly ovate to short- or very long-subrectangular, with *any* 1, 2, or all sides infolded near mouth, the perianth expanding slightly or moderately narrowing toward mouth, the mouth bilaterally compressed due to infolded lobes; lobes broadly rounded, *usually obscurely to distinctly bifid, the segments acuminate*, the mouth otherwise with several teeth, mouth occasionally with several narrowly or broadly rounded small accessory lobes.

Seta 7-12 cells in diameter, with 19-32 rows of outer cells with exposed walls moderately to very thick-walled surrounding an inner core of scattered cells that are slightly smaller than, or equal to, or slightly larger than outer row, the core cells with corners thickened similarly to small to medium trigones. Capsule elliptic, the valves 0.74-1.82 mm. long, 30-72 μ thick, of (3-)4-6 layers, the outer row of cells thicker than all of combined other strata or equal to a thickness of 2-3 $\times$ of interior strata; outer layer with red-brown, nodule-like to spinelike thickenings that are often very weakly tangentially dilated, with semiannular bands on some valves; exposed wall thickened; intermediate and inner layers of cells subequal in thickness, the intermediate layers with thickenings often distinctly extending onto tangential walls; inner layer of cells with red-brown semiannular bands very common on some valves, sporadic on others, the bands sometimes branched, often incomplete, the radial walls with nodulose thickenings very common on some valves, moderately represented on others.

Spores (10-)11-12(-13) μ, light brown, exine with the light microscope appearing minutely punctate, but under the SEM with a network of granulate to (more often) short, closely packed, vermiform projections densely covered with nanogranules; spores *averaging 1.1 $\times$ elater diameter*. Elaters (8-)9-11 μ wide, apical portions usually with thick nonspiral walls, red-brown.

KEY TO VARIETIES OF *Clasmatocolea obvoluta*

1. Dorsal leaf lobe *consistently* canaliculate and/or ventral leaf lobe *consistently* with a single conspicuous tooth on ventral margin; oil-bodies hyaline and glistening, consistently 2 per cell in leaf middle and apex as well as in underleaf. . var. *obvoluta*
1. Dorsal leaf lobe plane or occasionally with margins slightly reflexed, the ventral leaf lobe entire or occasionally with a single tooth on ventral margin; oil-bodies tannish to "dirty white," 2-3(-4) per cell in leaf middle, 2-4 in leaf apex, (2-)3-4(-5) in underleaf..... var. *cookiana*

Clasmatocolea obvoluta (Hook. f. & Tayl.) Grolle, var. **obvoluta.**

Jungermannia obvoluta Hook. f. & Tayl. London J. Bot. 7 30. 1845. *Lophocolea obvoluta* (Hook. f. & Tayl.) Evans, Bull. Torrey Bot. Club 25:421. 1898. *Clasmatocolea obvoluta* (Hook. f. & Tayl.) Grolle, Rev. Bryol. Lichénol. 29:72. 1960. Lectotype (*fide* Engel, 1976): Chile, Prov. Magallanes, I. Hermite, Cta. San Martin, *Davis s.n.* (FH!).

Jungermannia obvolutaeformis De Not. Mem. Reale Accad. Sci. Torino II. 16:220. *pl. 8, f. 1-4.* 1855, *syn. fide* Stephani (1906). *Lophocolea*

obvolutaeformis (De Not.) Mass. Nuovo Giorn. Bot. Ital. I. 17:223. 1885. Original material: Chile, "Prov. Valparaíso, Valparaíso," *Puccio* (*non vidi;* GE = O, NY = O, PAD = O, PC = O, RO = O, TO = O).

Dorsal leaf lobe *consistently* canaliculate and/or ventral leaf lobe *consistently* with a single conspicuous tooth on ventral margin; leaves usually 0.25-0.50-divided.

Differentiation.—*Clasmatocolea obvoluta* var. *obvoluta* is rather closely related to *C. trachyopa*. The relationship is especially evident when typical *C. obvoluta* is well developed and has strongly canaliculate dorsal lobes. The following characters of *C. obvoluta* var. *obvoluta* will serve to immediately distinguish it: (a) stems 9-18 cells high; (b) dorsal lobes medium- to wide-triangular; (c) ventral lobes medium- to very wide-triangular, with a single tooth on the ventral margin, but otherwise entire; and (d) underleaves nearly always connate on both sides and with apices 0.12-0.23-divided.

Notes.—1. *Clasmatocolea obvoluta*, like *C. trachyopa*, has a coelocaule precursor or swollen region on which the perianth and three series of bracts and bracteoles are inserted (fig. 15-1); see under *C. trachyopa* (p. 67) for further comments. In *C. obvoluta*, this phenomenon seems more closely related to the occurrence of fertilization than in *C. trachyopa*.

2. In some collections, the outer capsule walls have semiannular bands predominating but with nodulose thickenings rather common, whereas in other collections the walls have nodulose thickenings predominating and with semiannular bands very poorly developed.

Ecology.—Basically similar to that of var. *cookiana*, but seemingly with a somewhat wider ecological amplitude. In forests, like the other variety, it occurs on the floor and as a component of bryophyte mounds; var. *obvoluta*, however, also grows epiphytic on shrubs (*Pernettya* base, *Berberis illicifolia*, etc.) and tree branches. Particularly common as a component of vegetation over the small cliffs that are common in southern South American forests.

Phytogeography.—Tierra del Fuego and Patagonian Channels N. to 43° 57′ S. (I. Guaitecas). Hässel (1977) records the species for South Georgia; I have been unable to confirm or refute this report (see fig. 13).

Specimens seen.—**ARGENTINA.** TERR. TIERRA DEL FUEGO: I. de los Estados, *Spegazzini 21, 98, 99* as *L. obvolutaeformis* (VER); ibid., *Spegazzini 21, 99* as *L. obvolutaeformis* (NY); ibid., B. Blossom, *Spegazzini 24* as *L. obvolutaeformis* (VER); I. de los Estados, B. Crossley, *Hässel de Menéndez 3880* (BA, F); I. de los Estados, M. Richardson, *Spegazzini 159* as *L. obvolutaeformis* (VER). **CHILE.** PROV. MAGALLANES: Cabo

de Hornos, *sin. coll.* as *L. fulvella* (MICH); ibid., *Hooker s.n.* — c. per. (NY); Cta. San Martin, *Hooker 19d* (NY); ibid., *Davis s.n.* as syntype of *J. obvoluta* (S); ibid., I. Hermite, *Hahn s.n.* — c. per. as *L. obvolutaeformis* (PC, VER); I. Hermite, *Hooker s.n.* (NY); B. Tekenika, *Skottsberg s.n.* (S); I. Navarino, Angostura Murray, *Spegazzini 244* as *L. obvolutaeformis* (VER); I. Basket, *Spegazzini 3* (NY); ibid., S. Darwin, *Spegazzini 176*[2] as *L. obvolutaeformis* (VER); R. Azopardo, *Halle 221* (S); I. Capitan Arecena ("I. Clarence"), *Hariot s.n.* as *L. obvolutaeformis* (VER); I. Clarence, S. shore of B. Pond, *Engel 6264A* (MSC); I. Desolación, Pto. Angosto, *Dusén 161* as *L. lacerata* (NY, S); I. Desolación, Pto. Churruca, head of Br. Lobo, *Engel 5811* — c. ♂ (MSC); I. Desolación, Pto. Churruca, N. side of Fo. Nassau, *Engel 5890* — c. ♂, *5924* (MSC); I. Desolación, B. Tuesday, *Engel 5648* — c. sporo., *5713A* (MSC); B. Tuesday, *Naumann s.n.* as *L. obvolutaeformis* (FH); Brunswick Pen. (cf. Engel, 1978); E. side of B. Borja, *Engel 6130, 6144C, 6153, 6185* (MSC); B. Borja, *Voyage of Albatross s.n.* (FH); ibid., *Voyage of Albatross s.n.* as *L. obvolutaeformis* (NY); Can. Gajardo, Vo. Inga, *Halle & Skottsberg 221* (S); S. Skyring, Esto. Excelsior, *Halle & Skottsberg 221* — c. per. (S); Can. Smyth, *sin. coll.* as *L. trachyopa* (PC); Pto. Mayne, *Cunningham 169* (NY); E. side of Pto. Bueno, *Engel 5581A* (MSC); F. Peel, N. shore of Cta. Amalia, *Engel 5388A* (MSC); I. Chatham, N. shore of B. Wide, *Engel 5296A* — c. per., *5322, 5339* — c. sporo., *5363D* — c. per. (MSC); Pto. Alert, *Engel 4923C* (MSC); ibid., head of fiord W. of M. Markham, *Engel 4973* — c. ♂ (MSC). PROV. AISÉN: N. side of F. Témpano, *Engel 4381, 4386A, 4388C* (MSC); Pto. Island, *Cunningham 36* (BM); ibid., *Engel 4277* — c. ♂ (MSC); Pen. de Tres Montes, Pto. Barrosa [= Otway Harbor], *Challenger Exped. s.n.* (BM, NY); Pto. Puyuhuapi, R. Pascua, *Schwabe 37b* (JE); C. Tesoro, 800-900 m., *Schwabe 41/a* (hb. Grolle, JE) PROV. CHILOE: I. Guaitecas, *Dusén s.n.* as *L. trachyopa* (S); ibid., *Dusen 363* as *L. trachyopa* (JE).

Clasmatocolea obvoluta var. **cookiana** (Mass.) Engel.

Lophocolea cookiana Mass. Nuovo Giorn. Bot. Ital. I. 17:224. *pl. 16, f. 11.* 1885. *Clasmatocolea cookiana* (Mass.) Engel, J. Hattori Bot. Lab. 36:156. 1973. *Clasmatocolea obvoluta* var. *cookiana* (Mass.) Engel, Phytologia 41:311. 1979. Lectotype (*fide* Engel, 1973a): Argentina, Terr. Tierra del Fuego, I. de los Estados, Pto. Cook, February 1882, *Spegazzini 14* (VER! — c. ♂).

Lophocolea latissima Steph. Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26 (III, 6): 42. 1900, *syn. fide* Engel (1973a). Original material: Chile, Prov. Magallanes, S. Molyneux, 1 June 1896, *Dusén 68* (FH!, G!).

Dorsal leaf lobe plane or occasionally with margins slightly reflexed, ventral leaf lobe entire or occasionally with single tooth on ventral margin; leaves usually 0.15-0.25-divided.

Differentiation.—The leaves of *C. obvoluta* var. *cookiana* bear some resemblance to those of *C. rigens*, particularly when the latter are robust and considerably wider than long. There should, however, be no confusion between the taxa.

Note.—Stephani in his original description of *Lophocolea latissima* states in reference to the leaf: "postice haud longe libera ut in *Loph. cookiana* sed breviter inserta." The syntype of *Lophocolea latissima* and lectotype of *Clasmatocolea cookiana* both have underleaves connate on *both* sides with ventral leaf margins.

Ecology.—Rather common in mossy forests, where on the floor (often mixed with *Leptoscyphus horizontalis*, *Schistochila lamellata*, *Blepharidophyllum clandestinum*, *Megaceros endivaefolius*, etc.) or on the sides or apices of bryophyte mounds, often mixed or associated with *Blepharidophyllum densifolium*, *Leptoscyphus aequatus*, and *Adelanthus lindenbergianus*, etc. It also occurs on stream banks in moorland areas and over soil near waterfalls. It occasionally occurs mixed with *Sphagnum* in *Sphagnum* bogs.

Phytogeography.—Falkland Is.; Tierra del Fuego (including I. de los Estados and western portion); Patagonian Channels N. to 42° 39′ S.; mainland West Patagonia N. to 40° 45′ S. (see fig. 13).

Specimens seen.—**FALKLAND IS.** (selected). **EAST FALKLANDS:** Port Stanley, *Skottsberg 350* (S, UPS); Mt. Usborne Region, SE slope of Mt. Usborne 2, ca. 455 m., *Engel 2612C* (MSC). **ARGENTINA.** TERR. TIERRA DEL FUEGO: I. de los Estados, B. Crossley, *Hässel de Menéndez 3882* (BA, F); I. de los Estados, Pto. Cook, *Spegazzini 13* (G, VER); ibid., *Spegazzini 14* as *L. obvoluta* (NY). **CHILE.** PROV. MAGALLANES: I. Hornos, *Hariot 155* (VER); I. Desolación, *Dusén s.n.* (FH); ibid., *Dusén s.n.* as *L. obvoluta* (FH); ibid., Pto. Angosto, *Dusén s.n.* (S); ibid., *Dusén 265* (NY); ibid., *Dusén 401* as *L. latissima* (G); I. Desolación, Pto. Churruca, head of Br. Lobo, *Engel 4877B* (MSC); I. Desolación, B. Tuesday, *Engel 5695*, *5714*, *5742C* (MSC); Brunswick Pen. (cf. Engel, 1978 sub *C. cookiana*); B. Isthmus, *Savatier 205* (VER); E. side of Pto. Bueno, *Engel 5574* (MSC); Pto. Bueno, *Cunningham 143* as *L. obvoluta* (BM); head of F. Peel, *Engel 5492* (MSC); E. side of I. Juan, *Engel 5275C*, *5282B* (MSC); near E. shore of I. Pilot, *Engel 4756* (MSC); W. side of I. Grant, *Engel 4711* (MSC); head of inlet, Pto. Charrúa, *Engel 4866A* (MSC); Pto. Alert, *Engel 4939C* — c. per. (MSC); Pto. Edén, *Engel 4532B* — c. sporo., *4574A* — c. sporo. (MSC). PROV. AISÉN: N. side

of F. Témpano, *Engel 4391A* (MSC); Pto. Island, *Engel 4291* — c. ♂, *4296* (MSC); Istmo de Ofqui, Pta. Leopardos, *Hicken 62* as *L. obvoluta* (JE); R. Aisén, *Dusén 248* (NY). PROV. CHILOÉ: I. Guaitecas, *Dusén s.n.* as *L. trachyopa* (FH, NY — ♂, S — c. per.); ibid., *Dusén 12, 363, 371* as *L. trachyopa* (S); I. de San Pedro, *Dusén s.n.* as *L. obvoluta* (FH); ibid., *Dusén 576* as *L. obvoluta* (S); I. Chiloé, across Esto. Yaldad from village of Yaldad, Cocauque area, sea level, *Engel 11983* (F); I. Chiloé, E. of Cucao near SW end of L. Cucao, Loncomilla (Alto de la Virgen), 75 m., *Engel 12095, 12148B* (F). PROV. OSORNO: Near small lake 10.3 km. by road below Refugio Antillanca, 650 m., *Engel 11553* (F).

Clasmatocolea trachyopa (Hook. f. & Tayl.) Grolle. Figures 14-17, Plates 5-6.

Jungermannia trachyopa Hook. f. & Tayl. London J. Bot. 3:471. 1844. *Lophocolea trachyopa* (Hook. f. & Tayl.) G. L. & N. Syn. Hep. 699. 1847. *Clasmatocolea trachyopa* (Hook. f. & Tayl.) Grolle, Rev. Bryol. Lichénol. 29:73. 1960. Lectotype (*nov.*): Chile, Prov. Magallanes, I. Hermite, *Hooker* (FH! — c. sporo. + ♂).

Lophocolea arenaria Schiffn. *in* Naumann, Forschungsr. *Gazelle* 4 (4):13. *pl* 3, *f. 20-24*. 1890, *syn. fide* Stephani (1906). Holotype: Chile, Prov. Magallanes, Punta Arenas, 7 February 1876, *Naumann s.n.* (FH! — c. per.).

Lophocolea lacerata Steph. Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26 (III, 6):41. 1900, *syn. fide* Stephani (1906). Original material: Chile, Prov. Magallanes, Pto. Bueno, 31 May 1896, *Dusén 35* (NY!); Prov. Aisén, R. Aisén Valley, *Dusén* (FH!, G!, NY!, S! — 7 coll.).

Blepharostoma acanthifolium Gola, Nuovo Giorn. Bot. Ital. II. 29:169. *pl. 1, f. 18-19*. 1923, *syn. fide* Engel (1978). Original material: Chile, Prov. Magallanes, I. Laberinto, 5 February 1913, *Gasperi s.n.* (FI!).

Plants *somewhat hairy in appearance*, prostrate, mixed with other bryophytes or in dense, interwined, often pure, thick cushions, *pale grey-green or very pale green* or light brown tinged, often becoming brownish throughout in older collections; *main axes to 1.3 mm. wide.*

Branches *copiously produced*, often densely interwined, Frullania- *and lateral-intercalary type common*, the latter especially so; *ventral-intercalary type very rare.*

Stems 6-10 cells high, cortex in 1 row of slightly to distinctly thick-walled cells slightly smaller than, equal to, or larger than medullary cells, the cortex often with 1-2 rows of ventral cells smaller or equal in size to medullary cells, and with dorsal cortical cells larger than those of the medulla; medullary cell walls thin to slightly thickened; endophytic hyphae absent. Rhizoids in fascicles from stem near underleaf base.

Leaves with *insertion broad, narrow in weaker forms*, oblique, not or slightly recurved at ventral end; leaves strongly erect, approximate to densely imbricate, *ventral-median*

FIG. 14. *Clasmatocolea trachyopa* (Hook. f. & Tayl.) Grolle. **1,** Main axis with 3 lateral-intercalary branches (lib) and perianth on lateral branch. **2,** Distinctly bifid perianth lobes, ventral lobe in middle. **3,** Obscurely bifid perianth lobes, ventral lobe in middle. **4,** Antheridial stalk. **5,** Stem of main axis, cross section. **6,** Opposing antheridial bracts with stem(s), cross section. Figure 1, from *Engel 4850*, Chile, Prov. Magallanes, Pto. Charrúa; figure 2, from *Engel 6249*, Chile, Prov. Magallanes, B. Pond; figure 3, from *Engel 4381*, Chile, Prov. Aisén, F. Témpano; figures 4, 6, from *Engel 4814*, Chile, Prov. Magallanes, Pto. Charrúa; figure 5, from *Engel 5106*, Chile, Prov. Magallanes, I. Tarlton.

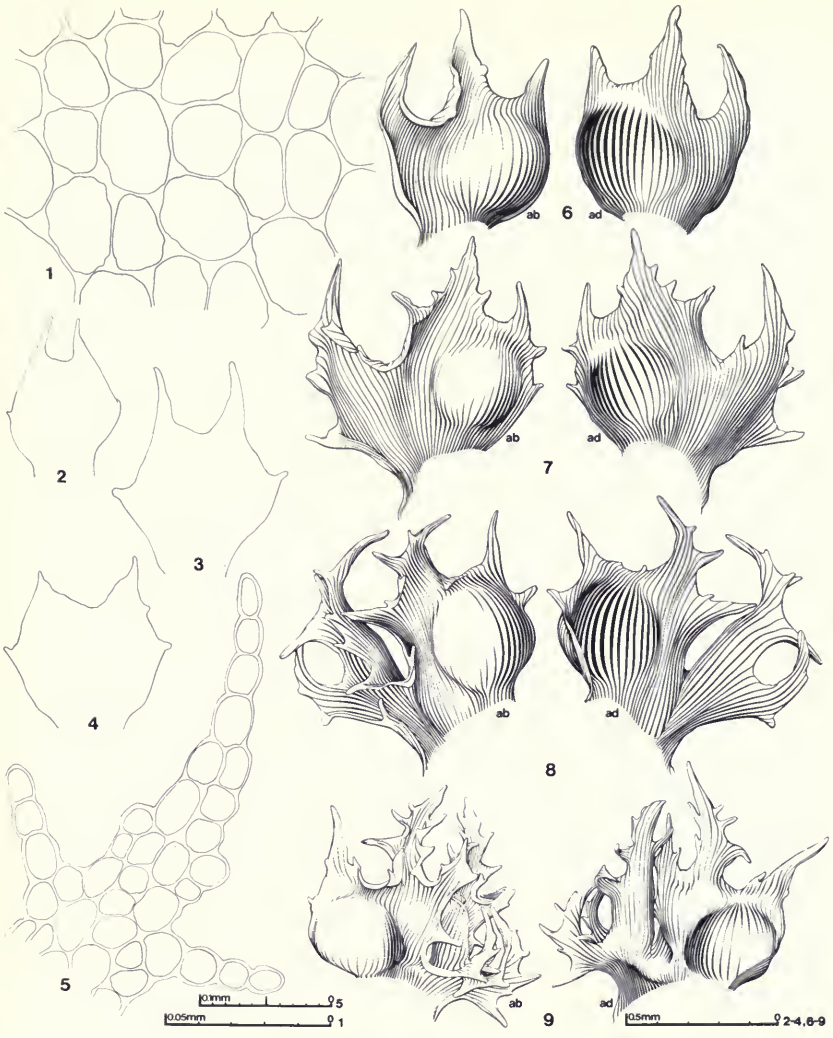


FIG. 15. *Clasmatocolea trachyopa* (Hook. f. & Tayl.) Grolle. **1,** Median leaf cells. **2-4,** Underleaves. **5,** Apical portion of median lobe of leaf showing submoniliform uniseriate portions. **6-9,** Leaves, abaxial (ab) and adaxial (ad) views (each number showing 2 views of same leaf); figures 1, 2, 6, 7, from type of *C. trachyopa*, *Hooker*, Chile, Prov. Magallanes, I. Hermite; figures 3, 5, from *Engel 4831*, Chile, Prov. Magallanes, Pto. Charrúa; figure 4, from *Engel 3985C*, Chile, Prov. Osorno, L. Toro; figure 8, from *Engel 4814*, Chile, Prov. Magallanes, Pto. Charrúa; figure 9, from *Engel 4134*, Chile, Prov. Osorno, R. Nauto.

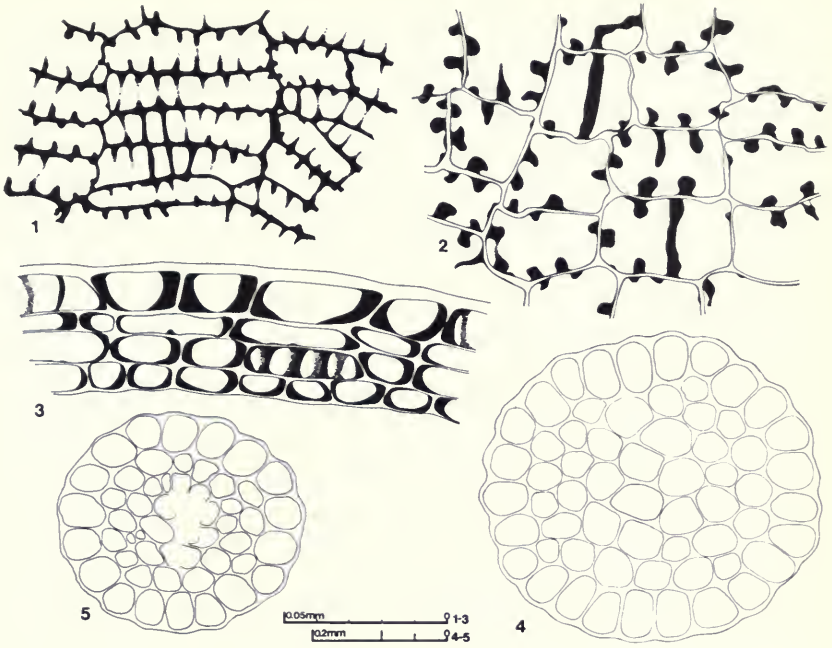


FIG. 16. *Clasmatocolea trachyopa* (Hook. f. & Tayl.) Grolle. **1,** Inner capsule wall cells. **2,** Outer capsule wall cells, note 2 semiannular bands. **3,** Capsule wall, cross section. **4, 5,** Setae; cross sections of two different setae from same collection. Figures 1, 3, 4, from *Engel 5203*, Chile, Prov. Magallanes, I. Madre de Dios; figure 2, from *Engel 4850*, Chile, Prov. Magallanes, Pto. Charrúa.

portion with a conspicuous, abrupt, concavity (the leaves often weakly concave in poorly developed axes), the leaves in abaxial view often with 2 elongate, sharp convexities that are proximal extensions of the canaliculate lobes; *leaves obscurely to distinctly obtrapezoid* or less often wide-ovate, basically *2-3-lobed*, but *often with 1-3 accessory lobes*, the **dorsal lobe** *acuminate*, erect or incurved in a broad bowlike arc, with *margins recurved and lending the lobe canaliculate*, often with margins connivent toward base and then lobe here locally tubiform; *dorsal lobe with several spinescent teeth or short cilia and often a few sharp laciniae* (which may be toothed), *the armature occurring in opposite pairs* but commonly with a few interspersed solitary teeth, the *dorsal-basal portion of dorsal lobe* (or more rarely the dorsal margin immediately proximal to lobe) *with a large tooth*, or dentate *lacinium*, or dentate, canaliculate *accessory lobe commonly situated at ± right angles to the dorsal lobe*, the armature nearly absent in depauperate axes, the uniseriate portions of dorsal lobe and lobe armature often submoniliform, the nonuniseriate portions often ± crenulate; **dorsal sinus** *0.5-0.75 the leaf length, deeper than ventral sinus*, the tissue at sinus base frequently recurved at the base and often with 1-2 spinescent teeth; **median lobe** (in basically *trifid* leaves, or ventral lobe

FIG. 17. *Clasmatocolea trachyopa* (Hook. f. & Tayl.) Grolle.

in *bifid* leaves) ± *acuminate to narrowly triangular*, erect or incurved in a broad bow-like arc, *with margins often recurved* lending the lobe *canaliculate*, the median lobe with characters of armature as in the dorsal lobe; **ventral sinus,** when present, 0.25-0.5 the leaf length, the tissue at sinus base plane or recurved, often with a tooth; **ventral lobe** (in *trifid* leaves) variable in size, much smaller than dorsal or median lobe, the margins plane or recurved and then lobe at most moderately canaliculate, the lobe entire or with a few pairs of opposite teeth, the uniseriate portion often submoniliform; **dorsal margin** of lamina *usually* ± *straight* or occasionally rounded near base, *recurved,* entire or with a few teeth, short decurrent; **ventral margin** of lamina plane or if incurved, then with ventral portion of leaf ± saccate, the ventral margin *narrowly or broadly rounded,* with a tooth or lacinium near base of lobe, the margin otherwise entire or with a few teeth or laciniae.

Leaf cells thin to moderately thick-walled, trigones small to large and bulging; median leaf cells of disc 17-36 μ wide, 18-48(-53) μ long; cuticle smooth or slightly roughened and appearing finely granular.

Underleaves *1.3-2(-3.5)* × *stem width*, free or connate on 1 side, slightly to moderately spreading, approximate to densely imbricate, plane to moderately convex (ventral view) but not abruptly so, the margins occasionally curved ventrally, especially so toward base; underleaves *ovate*, rarely subrhomboid, with *apices 0.25- to slightly less than 0.5-bifid;* segments with *uniseriate portion often* ± *submoniliform*, terminating in a slime papilla, the segment margins entire; margins of the lamina entire to 3-dentate-small laciniate, the armature often terminating in a small slime papilla. Branch underleaves strongly spreading, deeply convex to ± cupulate.

Plants dioecious; androecia terminal or intercalary on main axis or abbreviated to long lateral-intercalary or *Frullania*-type branches; bracts with basal portion strongly saccate, the *saccate portion fused toward base with opposite bract*, the distal portion of bract with lobes and lobe armature as in leaves, or if bracts bifid, then with lobes plane, entire, and with ventral margin broadly rounded and entire or 1-dentate; lobule margin involute, with several slime papillae and often few-celled teeth, or with 1 lacinium or broadly rounded involute lobe; antherida solitary, stalk uniseriate.

Gynoecia usually on short, abbreviated lateral-intercalary branches, very rarely on main axis; subfloral innovations absent or when present (rare) from below innermost bract, the innovations very short and producing a perianth; *coelocaule precursor present;* bracts and bracteoles in 3 series, *inserted on coelocaule precursor;* **bracts** of innermost series slightly convex or concave, especially in upper portion, obovate to subspatulate to occasionally wide-ovate; *apices 2-3-lobed, if bifid, then divided to slightly over 0.5, or if trifid (occasional), then dorsal sinus extending to slightly over 0.5 bract length and the ventral sinus to 0.3 bract length;* dorsal lobe with margins consistently reflexed, occasionally strongly so and then lobe locally tubiform; ventral lobe and, when present, median lobe occasionally with margins reflexed, occasionally strongly so and then lobe(s) locally tubiform; apex of lobes with several small to large and spinescent teeth or short cilia (and occasionally a dentate lacinium), the teeth and cilia in opposite pairs, the dorsal-basal portion of dorsal lobe (or more rarely dorsal margin immediately proximal to lobe) usually with a small dentate, occasionally canaliculate lobe, the accessory lobe occasionally absent and then bract commonly ± bilaterally symmetric; lamina margins with several teeth, especially in upper portion. **Bracteoles** of innermost series subequal to bracts in size, free from bracts, slightly convex, or slightly to distinctly concave (ventral view), the bracteoles elliptic to obovate to subspatulate; *apices*

0.2-0.4-bifid; segment margins plane or if reflexed, then with lobes moderately to strongly canaliculate, with several small to large and spinescent teeth or short cilia (and occasionally a dentate lacinium), the teeth and cilia in opposite pairs; lamina margins with several small teeth (especially in upper portion), often with a small lobe in upper portion. **Perianth** *strongly trigonous, narrowly ovate to narrowly elliptic to elongate-subrectangular,* commonly with 2 or all 3 sides wholly or in part infolded near mouth, but occasionally only with ventral side strongly infolded, the perianth gradually narrowing or straight or gradually expanding toward mouth, the mouth compressed due to infolded lobes, occasionally bilaterally so; lobes broadly rounded, *usually obscurely to distinctly bifid,* the *segments narrowly acuminate* and *often with margins reflexed,* occasionally strongly so and lobe locally tubiform, the *segment margins armed with a few to several pairs of opposite teeth,* the lobes otherwise with several teeth and elongate cilia; lobes occasionally undivided, and then either with a few small teeth, or copiously dentate to elongate-ciliate and with a few small, dentate, accessory lobes; wings often present, of several cells high and occasionally with a few teeth.

Sporophyte with foot "penetrating" into axial proliferated tissue to level of ca. bract of first series or first leaf below. Seta (6-)7-9 cells in diameter, with 17-30 rows of outer cells with inner corners thickened similarly to medium to large and bulging trigones, the inner core of cells considerably smaller than or subequal to outer row in size, the core cells gradually increasing in size toward center, the core cells thin-walled, with corners thickened similarly to small to medium trigones. Capsule ± globose to elliptic to ovate, the valves 0.7-1.15 mm. long, 29-48(-52) μ thick, of (3-)4(-5) layers, outer row of cells equal to thickness of 1.8-2.5(3) of interior strata; outer layer with vinaceous, nodule-like or spinelike thickenings that are often feebly tangentially dilated, a few to several semiannular bands present; exposed wall thickened; intermediate and inner layers of cells subequal in thickness, the intermediate layers with thickenings often considerably tangentially dilated; inner layer of cells with red-brown semiannular bands, the bands often nonpigmented in median portion, incomplete, the radial walls with nodulose thickenings often present.

Spores 11-14 μ, light brown, exine with the light microscope appearing minutely punctate, but under the SEM with a network of very wide, irregular, coalescing vermiform ridges; spores averaging 1.4 × elater diameter. Elaters 6-11 μ wide, apical portions often with thick nonspiral walls, elater walls red-brown or yellow-brown.

Differentiation.—Clasmatocolea trachyopa is rather closely related to *C. obvoluta* var. *obvoluta;* for further notes regarding this relationship see p. 57. *Clasmatocolea trachyopa* represents the culmination of a trend in leaf complexity in Subg. *Lacerifolia* beginning with *C. obvoluta* var. *cookiana,* through *C. obvoluta* var. *obvoluta* to *C. trachyopa.*

Specimens of *C. trachyopa* may be identified at once by the very distinctive general aspect of the plant (see fig. 14-1). The dorsal and median leaf lobes are usually canaliculate due to the recurved margins. As a result of these recurved margins, the opposing pairs of lobe armature are ventrally oriented and at right angles to the leaf lamina plane. Conspicuous also is the commonly dentate and canaliculate lacinium or lobe at the dorsal-basal portion of the dorsal lobe. This lacinium or lobe usually projects at right angles to the dorsal lobe but may arc toward the dorsal lobe. No

other species of *Clasmatocolea* has the degree of leaf complexity observed in *C. trachyopa*. For example, both the development of a three-lobed leaf as well as accessory lobes at leaf apex and margins are unique to the genus.

Notes.—1. A problem of typification arises from the fact that the original material of *Jungermannia trachyopa* deposited in the Farlow Herbarium (hb. Taylor) is a mixture of two *Clasmatocolea* species—a few stems of *C. obvoluta* that are sterile and a comparatively large amount of *C. trachyopa* that has both perianths and sporophytes. The sheet on which the specimens and packet are mounted bears hand-drawn illustrations of (a) a portion of an axis with two leaves and an underleaf; (b) an underleaf; (c) a perianth; and (d) a perianth cross section. Although it is obvious that that portion of the original description dealing with the perianth and sporophyte in Hooker & Taylor (1844) pertains to *C. trachyopa*, I am uncertain whether the description of sterile gametophyte structures pertains to *C. obvoluta* or poorly developed axes of *C. trachyopa* (which are present in the type collection). This is particularly the case because the description of the gametophyte matches the figure of the leaves and underleaf on the herbarium sheet, and this figure appears much like *C. obvoluta*. Further, a syntype of *J. trachyopa* deposited in the Stockholm Herbarium (S, ex hb. Lehmann) consists solely of a few stems of *C. obvoluta* with no *C. trachyopa* present. However, Taylor & Hooker (1847) have effectively typified the species because their description of *Jungermannia trachyopa* clearly refers to plants with 2-3-lobed, unequally spinose-dentate leaves, and the illustrations for the species clearly show spinose-dentate leaves. Both the description and illustrations exclude material of *C. obvoluta*. I have selected the material of *C. trachyopa* as lectotype, because the rules state [I.C.B.N. (1972, p. 76)]: "In choosing a lectotype, any indication of intent by the author of a name should be given preference unless such indication is contrary to the protologue" (see also I.C.B.N., Art. 70).

2. As mentioned above, some of the axes in the lectotype collection are depauperate. In these axes the leaves are only slightly concave, the margins of the dorsal and median lobes are only slightly reflexed, the lobes are entire or have one opposing pair of teeth, and the basal-dorsal portion of the dorsal lobe is entire or has one small tooth (*i.e.*, the leaves lack the conspicuous lacinium or lobe that commonly projects at right angles to the dorsal lobe) (see fig. 15-6). The depauperate condition is rather rare.

3. *Clasmatocolea trachyopa*, like *C. obvoluta*, possesses a coelocaule precursor. In *C. trachyopa* there is a swollen region on which the perianth and three series of bracts and bracteoles are inserted. The sporophyte

"penetrates" to about the level of the bracts of the first series or the leaves immediately below.

4. This species, like *C. obvoluta*, has androecial bracts with saccate portions fused toward the base with the bract on the opposing side of the stem (fig. 14-6). This condition totally obliterates a dorsal view of the stem.

5. All observed 1897 Dusén specimens labeled *Lophocolea trachyopa* from Islas Guaitecas are misdeterminations of *C. obvoluta* var. *obvoluta* or *C. obvoluta* var. *cookiana*.

Ecology.—On rotted logs and stumps (often those covered with bryophytes) or occasionally corticolous on trees in forests, commonly where there is at least moderate amounts of shade. It sometimes occurs with *Lepidolaena magellanica* or *Clasmatocolea humilis*, but more often it is associated with *Riccardia* sp.

Phytogeography.—Tierra del Fuego (including I. Grande de Tierra del Fuego); Patagonian Channels; Valdivian region (100-885 m.) N. to 39° 56′ S. (Prov. Valdivia) (see fig. 17).

Specimens seen.—**ARGENTINA.** TERR. TIERRA DEL FUEGO: I. de los Estados, *Spegazzini 44*[2], *99*[1] (VER); ibid., Pto. Cook, *Spegazzini 28*[1] (VER); ibid., *Spegazzini 45*[2] (NY, VER); ibid., *Spegazzini 320* (VER). **CHILE.** PROV. MAGALLANES: Cabo de Hornos, *Hooker s.n.* as syntype of *J. trachyopa* (NY); (western) L. Fagnano, *Skottsberg 235* (S); I. Clarence, S. shore of B. Pond, *Engel 6249* — c. sporo. + ♂, *6283* — c. sporo. + ♂ (MSC); I. Desolación, *Dusén s.n.* as *L. lacerata* (S); ibid., Pto. Angosto, *Dusén 256* as *L. lacerata* — c. per. (S); I. Desolación, Pto. Churruca, N. side of Fo. Nassau, *Engel 5942* — c. sporo. + ♂ (MSC); I. Desolación, B. Tuesday, head of inner harbor, *Engel 5716* (MSC); Brunswick Pen. (cf. Engel, 1978); E. side of B. Borja, *Engel 6174* — c. sporo. (MSC); S. Skyring, Esto. Excelsior, *Halle & Skottsberg 235* — c. per. (S); NE corner of I. Tarlton, *Engel 5106* — c. sporo. (MSC); S. side of I. Madre de Dios, N. of I. Tarlton, *Engel 5203A* — c. sporo. (MSC); S. side of I. Madre de Dios, head of fiord E. of M. Roberto, *Engel 5150*, *5151A* (MSC); Pto. Charrúa, *Engel 4805* — c. sporo. + ♂, *4814* — c. ♂, *4831* — c. sporo., *4836*, *4850* — c. sporo., *4860* (MSC). PROV. AISÉN: Pen. de Taitao, Cabo Tres Montes, Pto. Barroso, *Roivainen 1644b* (H); L. Risopatron, *Schwabe 6/d* (hb. Grolle). PROV. CHILOÉ: Pto. Ballena, *Engel 4167B* — c. sporo., *4232* — c. sporo. (MSC); I. Chiloé, Cord. San Pedro, near aserradero at San Pedro, R. Puidi, 320 m., *Engel 11902* (F); I. Chiloé, Cord. San Pedro, Butalcura, near R. Butalcura, 11 km. by road from Ruta 5, 100 m., *Engel 11812* (F). PROV. OSORNO: Around L. Toro on road to Refugio Antillanca, 855-885 m., *Engel 3969*, *3979B*,

3985C — c. per. + ♂, *4005*, *4013*, *4020A* — c. sporo., *4042C* — c. per. (MSC); below L. Toro on road to Refugio Antillanca, near R. Nauto, 825 m., *Engel 4134* (MSC); 12.1 km. by road below Refugio Antillanca, 550 m., *Engel 11534* (F); Agua Caliente, along R. Chanleufú, 4 km. from Termas de Puyehue along road to Refugio Antillanca, 400 m., *Engel 11468* — c. ♂, *11477* — c. per. (F); Anticura, near Salto del Indio, 19 km. by road E. of Termas de Puyehue, 300 m., *Engel 11669* — c. per. (F); Huitrapulli, Aleucapi, 700-820 m., *Schwabe s.n.* — c. per. (hb. Schuster); ibid., *Schwabe 28* — c. ♂ (JE). PROV. VALDIVIA: W. slope of Cord. Pelada, W. of El Mirador, between La Union and Pta. Hueicolla, 580-680 m., *Engel 12255*, *14324* (F); E. slope of Cord. Pelada, E. of El Mirador, between La Union and Pta. Hueicolla, 740-840 m., *Engel 12466* — c. per., *14432* (F); Chaihuín, Pto. Colun, ca. 500 m., *Schwabe 6/g* (hb. Grolle); ibid., *Schwabe 26*, *26h* (JE).

Subg. **CLASMATOCOLEA**

Leaves undivided, entire or variously armed; underleaves of main axis and branches conspicuous, not reduced, free or connate on 1 side; androecia narrower than sterile portion of axis, the bract lobules entire, dentate or with 1 lacinium or lobe; bracteoles free from bracts; perianth without scales or plicae, the lobes broadly rounded, undivided.

Distribution.—Pan-temperate, occurring in all three sectors of Southern Hemisphere; in American sector north in Andes to Costa Rica, in African sector north to Burundi, and in Australasian sector disjunct in Java.

Sect. **PACHYCLASMATOCOLEA** Engel, sect. nov.

Foliorum caulina laminae 2-4-stratosae in media-basis parte; foliorum et interdum amphigastriorum margines conspicue incrassatae, 2-4-stratosae; antheridii pedicelli 4-seriati.

Type species: *Clasmatocolea marginata* (Steph.) Grolle.

Leaf lamina 2-4-stratose in median-basal area; leaf and sometimes underleaf margins conspicuously swollen, the elevated border 2-4-stratose; antheridial stalks 4-seriate.

Distribution.—Endemic to Tasmania.

Clasmatocolea marginata (Steph.) Grolle. Figures 18-20.

Jungermannia marginata Mitt. *in* Hooker, Bot. Antarc. Voy. 3:222. 1859 *non J. marginata* Lehm. Nov. Minus Cogn. Stir. Pug. 5:11. 1833 (= *Cololejeunea*), *non J. marginata* Hook. f. & Tayl. London J. Bot. 3:566. 1844 (= *Radula*). *Leioscyphus marginatus* Steph. Bull. Herb. Boissier 6 (3):223. 1906 (= Spec. Hep. 3:23). *Odontoschisma marginatum* (Steph.) Steph. Bull. Herb. Boissier 8 (8): 594. 1908 (= Spec. Hep. 3:378) ≡ *Clasmatocolea crassimarginata* Grolle, Rev. Bryol. Lichénol. 29:71. 1960. *Clasmatocolea marginata* (Steph.)

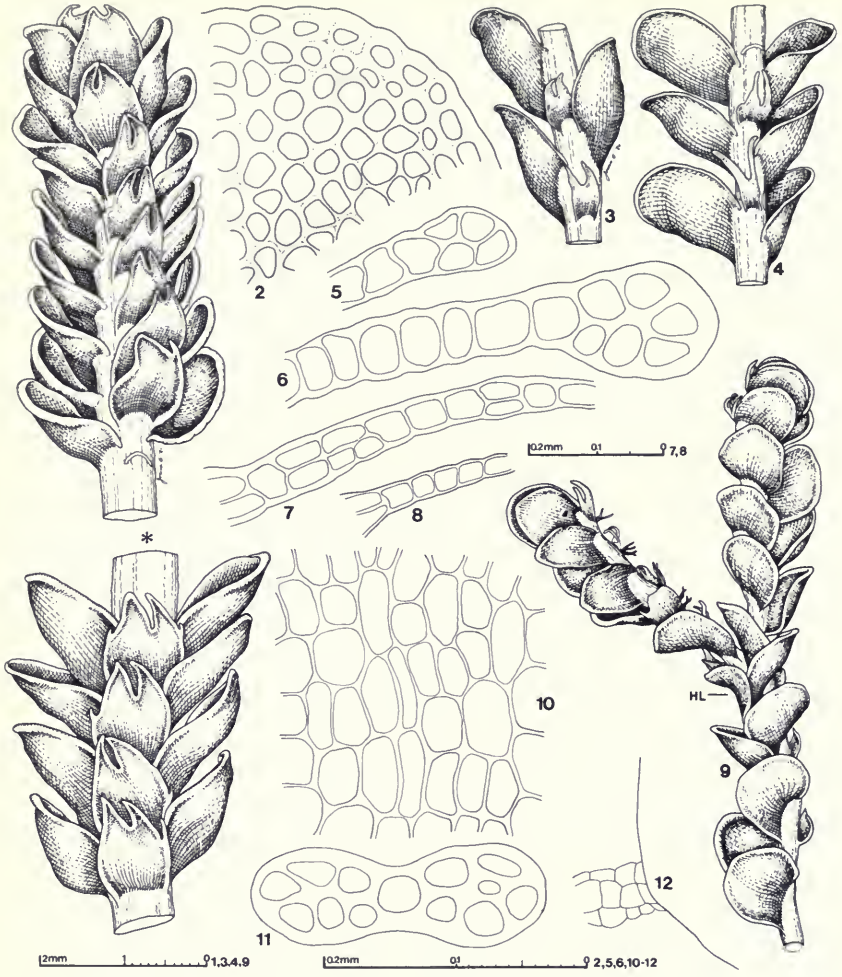


FIG. 18. *Clasmatocotea marginata* (Steph.) Grolle. **1,** Main axis, ventral view. **2,** Stem, cross section. **3, 4,** Portion of main axis, ventral view. **5, 6,** Underleaf, cross section through marginal area. **7, 8,** Underleaf, longisection through median-basal area of lamina. **9,** Axis, dorsal view with *Frullania*-type branch and associated half-leaf (HL). **10,** Median leaf cells. **11,** Underleaf segment, cross section. **12,** Antheridial stalk (the fourth row not in plane of view). Figures 1, 6, 7, 11, from *Engel 14328*, Tasmania, Mt. Field Natl. Park, Mt. Mawson Plateau; figures 2-5, 9, 10, from lectotype; figure 12, from *Rodway*, Mt. Wellington Plateau.

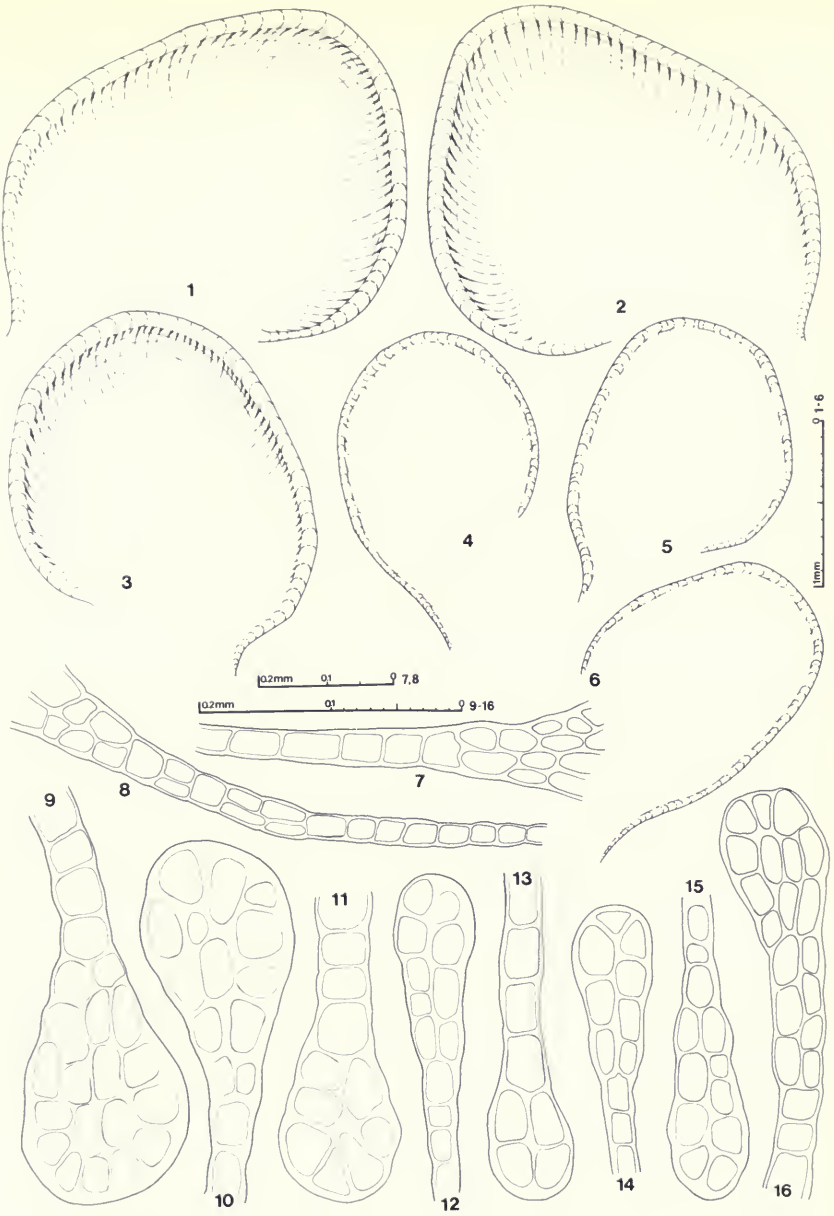


FIG. 19. *Clasmatocolea marginata* (Steph.) Grolle. **1-6,** Leaves (1-3, not flattened, 4-6, flattened). **7, 8,** Leaves, longisection through median-basal area. **9-16,** Leaves, longisection through apex. Figures 1-3, 7, 9-11, from *Engel 14328*, Tasmania, Mt. Field Natl. Park, Mt. Mawson Plateau; figures 4-6, 8, 12-16, from lectotype.

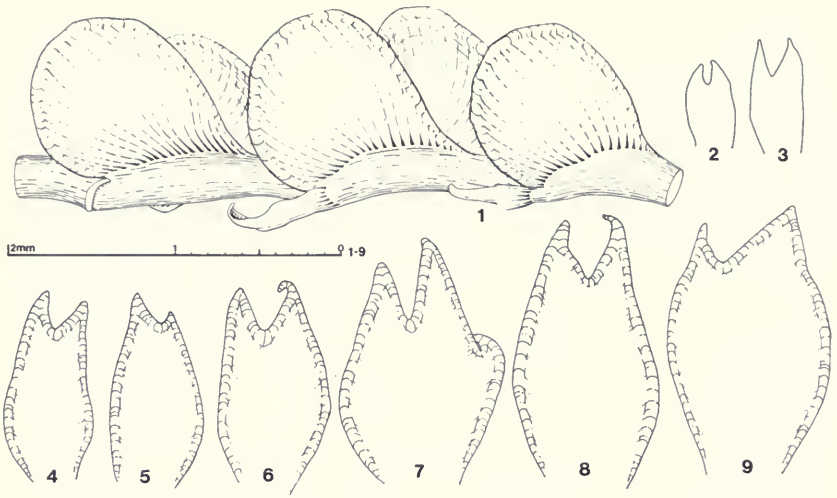


FIG. 20. *Clasmatocolea marginata* (Steph.) Grolle. **1,** Portion of axis, lateral view. **2-9,** Underleaves. Figures 1-3, from lectotype; figures 4, 5, from *Rodway*, Mt. Wellington Plateau; figures 6-9, from *Engel 14328*, Tasmania, Mt. Field Natl. Park, Mt. Mawson Plateau.

Grolle, Nova Acta Leop. 25 (161):73. 1962. Lectotype (*nov.*): Tasmania, Arthur's Lakes, 13/2/43, *sin. coll.* (*Gunn*) *1648* (NY!).

Plants *very stiff, rigid, wiry, fleshy, erect*, in pure tufts; axes to 12 cm. tall, to 3 mm. wide, *brown to brownish black, highly nitid.*

Branches rather frequent, *of* Frullania- *lateral-intercalary and ventral-intercalary types*, the intercalary branches a bit more common; main axis and branches occasionally becoming flagelliform, the flagelliform portions with leaves scaly and distant or with leaves caducous.

Stems 14-15 cells high, cortex in 1-2 rows of smaller cells with thicker walls, the epidermal row with the outer tangential and often also the radial walls brownish; medullary cell walls thick; endophytic hyphae not seen. Rhizoids only sporadically developed, in fascicles at underleaf bases.

Leaves rigid, fleshy, brittle, the margins appearing conspicuously swollen, the distal (2-)4-6(-7) cell rows 2-4-stratose and forming a slightly to distinctly elevated border, the margin swollen its entire length, but less conspicuously so toward the leaf bases; leaf margin *in cross section* with the multistratose portion forming a knotlike swelling sharply defined from the leaf lamina or the multistratose portion gradually merging with the lamina, the marginal cells not appreciably differing in size from neighboring cells, but with thicker walls; *leaf lamina 2-4-stratose in median-basal area, the lamina otherwise unistratose*, except for occasional local bistratose areas; leaf insertion slightly recurved at ventral end; leaves erect to spreading, contiguous to imbricate, moderately to rather deeply adaxially concave, ovate to suborbicular, the apex broadly rounded to subtruncate, undivided, *the apex and margins entire;* dorsal margin slightly to distinctly rounded, plane, short to long decurrent on well-developed axes; ventral margin distinctly rounded, rather sharply so toward the base, plane.

Leaf cells with *walls slightly thickened, trigones small;* median leaf cells 24-38 μ wide, 36-53(-60) μ long; cuticle roughened.

Underleaves stiff, rigid, 0.65-1.5 × stem width, the margins (both lamina and segment) unistratose *or multistratose and then appearing slightly swollen, the marginal (1-)2-4 cell rows bistratose, forming an inflated,* sometimes knotlike, *thick-walled group of cells; underleaf lamina bistratose toward the base,* the lamina otherwise unistratose, except for occasional local bistratose areas; underleaves free, but in close proximity to leaf on 1 side, slightly spreading, distant to imbricate, plane or slightly convex, the segments often curved toward stem (sometimes sharply so), the *underleaves elliptic to subrectangular to narrowly ovate; apices bifid 0.15-0.45; segments frequently of different size and configuration,* narrowly or broadly triangular, the tips acute or rounded, sometimes acuminate, the segment margins entire; *margins of the lamina entire or with one tooth.*

Plants dioecious; androecia terminal or intercalary on leading axes; *bracts nearly obliterating view of dorsal surface of stem,* with basal portion saccate, the distal portion strongly concave, with apices appressed to bract immediately above; lobe margins with an elevated border similar to leaves; lobule margin incurved, with a small tooth or rounded projection, or entire; antheridia 1(-2) per bract, *stalk* short, *of 4 cell rows.*

Gynoecia and sporophyte not seen.

Variation.—The lectotype represents a smaller facies of the species, with less than optimal expression of characters. Among the notable differences, *robust* plants have (a) a lesser tendency for axes to become flagelliform; (b) leaves short decurrent, more often erect, more closely imbricate and more deeply concave; (c) leaf borders more pronounced and composed of a greater number of cells; (d) leaf bases composed of a greater number of strata; (e) underleaves contiguous to imbricate and, on the whole, less shallowly divided; and (f) underleaf borders more swollen and conspicuous.

Differentiation.—This species is at once distinct from all other members of the genus in possessing swollen, elevated leaf and (often) underleaf margins, which in section are 2-4-stratose. In fact, the only other leafy hepatic with multicellular leaf margins known to me is *Wettsteinia densiretis* (cf. Grolle, 1965). The species is also unique within *Clasmatocolea* in (a) the median-basal polystraty of leaf and underleaf lamina; and (b) the 4-seriate antheridial stalks. The collection of these features necessitates a somewhat isolated position within Subg. *Clasmatocolea;* the closest relative of the species appears to be *C. humilis* of Sect. *Clasmatocolea.*

Ecology-Phytogeography.—Rare endemic to Tasmania, where submerged or semisubmerged over rock in lakes or cold, rather rapid moving water of creeks at 950-1,300 m.

Specimens seen.—**TASMANIA:** Mt. Wellington Plateau, *Rodway s.n.* (HO); Wellington Falls, *Bastow 349* (MEL); Brown's R., *Oldfield* (MEL); Mt. Field Natl. Park, Mt. Mawson Plateau, W. of L. Dobson and S. of L. Seal, 1,250 m., *Engel 14328* (F); Ben Lomond Natl. Park, L. Youl, *A. Ratkowsky 79/4* (F); Cradle Mt. Region, Shadow L., ca. 950 m., *Norris 27792* (F).

Sect. CLASMATOCOLEA

Intercalary branches basically similar to main axis, the branches not vermiform or submoniliform (exc. *C. moniliformis*), usually of same width as main axis, often very long; leaves and underleaves unistratose throughout, the margins not swollen or elevated; leaf cuticle smooth or slightly roughened; antheridial stalks 1-2-seriate.

Distribution.—Pan-temperate; in American sector north in Andes to Costa Rica, in African sector north to Burundi.

Clasmatocolea humilis (Hook. f. & Tayl.) Grolle. Figures 21-24. Plates 7-10.

For synonymy see under varieties.

Plants fleshy and often soft to rather stiff and wiry, prostrate to suberect, mixed with other bryophytes, or in dense intertwined often pure mats, *grey-green to olive-green to light to deep brown*, rarely light green, the stems commonly red-brown; axes to 7.3 cm. tall, to *1.8 mm. wide*.

Branches common, occasionally in irregular fascicles, *commonly of lateral- and ventral-intercalary type, the lateral-intercalary more prevalent;* lateral-intercalary branches from ventral portion of leaf axils or directly basiscopic to stem leaves; Frullania-*type branches occasional* but more common in hygrophilous forms; branches occasionally with first leaf or first pair of leaves retuse to short-bifid, especially on intercalary branches; stolons very exceptional [only a single ventral-intercalary stolon seen (*Engel 5304A*)].

Stems *8-14 cells high*, the cortex in 1-2(-3) rows of moderately to distinctly thick-walled cells smaller than (or very rarely equal in size to) medullary cells; exposed wall of outer cortical row moderately to very thickened; medullary cell walls thin to slightly thickened; endophytic hyphae absent. Rhizoids in fascicles from stem near underleaf base.

Leaves with insertion very slightly to distinctly recurved at ventral end; leaves strongly erect, dorsally connivent, often lending axis a somewhat vermiform appearance, the leaves occasionally moderately spreading, loosely to densely imbricate, conchiform concave, *orbicular to oblate to subreniform;* apex broadly rounded to truncate, very rarely broadly retuse, undivided, often moderately to distinctly inflexed, sometimes ca. upper half of leaf moderately inflexed; *apices and margins entire, or with a few sporadic teeth, or regularly dentate;* dorsal margin ± straight in proximal half, plane to sinuous, rarely reflexed, not to rather long decurrent; ventral margin plane or moderately inflexed, broadly rounded, the basal portion often enlarged to ± auriculate, often extending ventrally beyond stem and in contact with slightly spreading underleaf, occasionally in contact with ventral margin of opposite leaf.

Leaf cells *thin-walled, trigones large to bulging to knotlike*, occasionally confluent, occasionally minute to medium in hygrophilous facies; median leaf cells 11-26(-30) μ wide; 12-32(-38) μ long; cuticle smooth or slightly roughened. Oil-bodies throughout leaf, occupying small fraction of cell lumen, hyaline to very light grey, of grape-cluster type, with numerous, small, slightly protruding globules, the oil-body surface appearing coarsely papillose; oil-bodies subglobose to ovoid to elliptic to fusiform in shape, consistently 2 per cell of leaf middle and apex, and 2-5 of leaf base, those of leaf middle 3-4 μ wide, 5-8(-10) μ long; oil-bodies throughout underleaf, 2(-3) per cell, of same size as those of leaf middle.

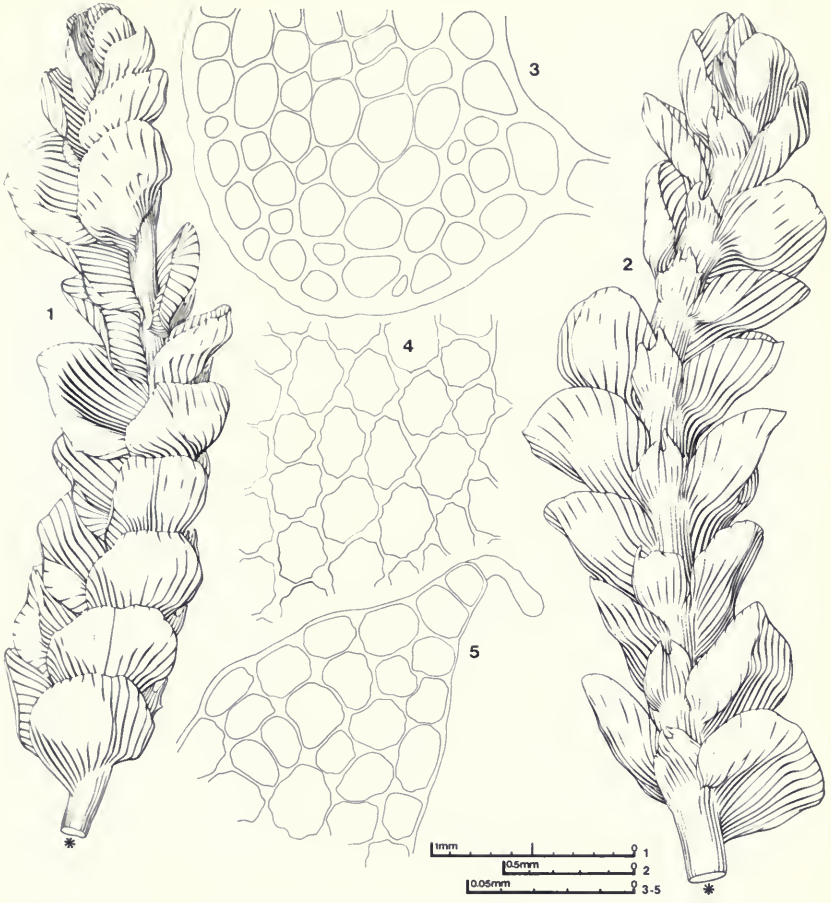
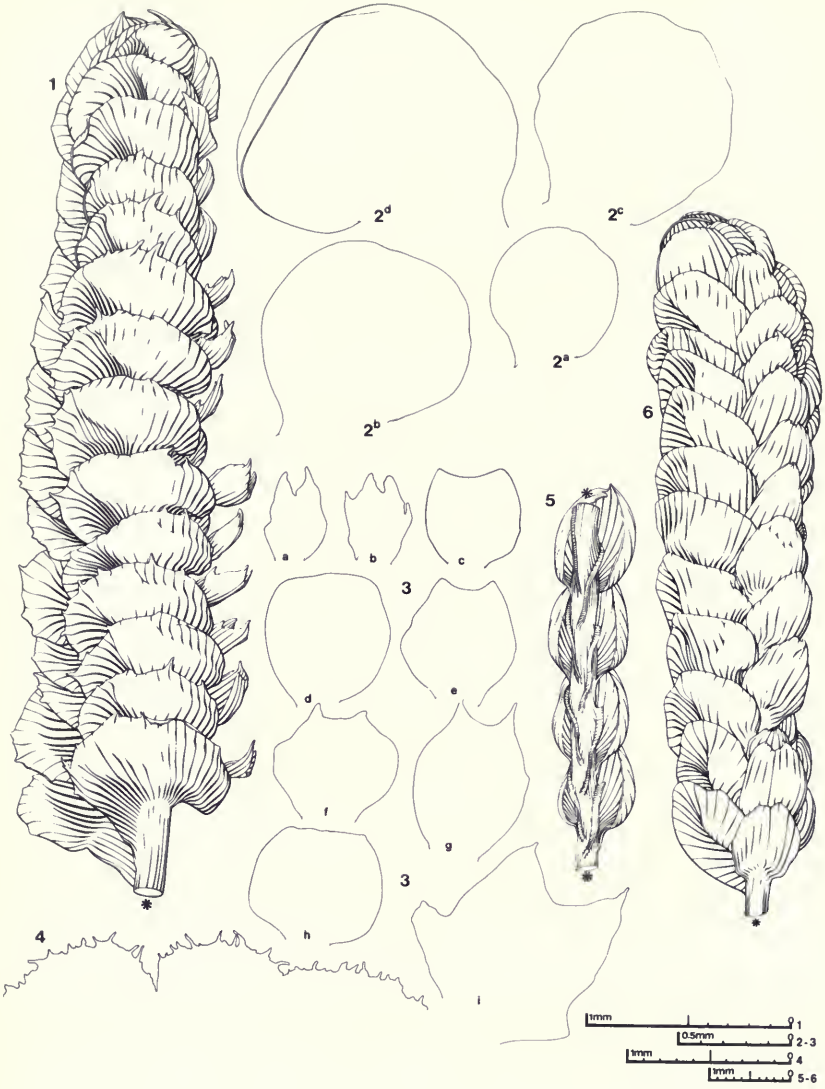


FIG. 21. *Clasmatocolea humilis* (Hook. f. & Tayl.) Grolle. **1,** Main axis, dorsal view, **2,** Main axis, ventral view. **3,** Stem, cross section. **4,** Median leaf cells. **5,** Underleaf segment, apical portion with slime papilla. Figures 1-3, from lectotype of *C. humilis*, *Hooker*, Kerguelen; figures 4, 5, from syntype of *C. humilis*, *Hooker*, Kerguelen (S).

Underleaves *1-4.3(-4.8)* × *stem width*, free or connate on 1 side, transversely or obliquely inserted, appressed to stem or slightly to strongly spreading (and then at nearly right angles to stem); underleaves distant to imbricate, *very slightly convex to deeply convex* (ventral view) and then with margins curved dorsally and often strongly incurved, the underleaves occasionally ± cupulate, the basal portion often abruptly convex; underleaves orbicular to oblate to ovate to elliptic to subrectangular, with basal portion occasionally subauriculate; *apices undivided and broadly rounded to truncate, or bidentate to broadly retuse to bifid to 0.35*, the apices very rarely only with 2 slime papillae; segments often of different size and configuration, occasionally apiculate, occasionally terminating in a slime papilla, the segment margins entire; lamina


1
2d
2c
2a
2b
6
5
a
b
c
3
d
e
f
g
3
4
h
i
1mm
1
0.5mm
2-3
1mm
4
1mm
5-6

margins with 1 slime papilla or tooth or lobe terminating in a slime papilla, *the margins occasionally entire.*

Plants dioecious; androecia terminal or intercalary on main axis or short to rather long lateral- or ventral-intercalary branches; bracts with basal portion strongly saccate and distal portion slightly to strongly concave, with bract apices appressed to bract immediately above or moderately spreading; lobule margin involute, with armature variable: with 1-several slime papillae and often few-celled teeth, or with 1 lacinium or large, broadly rounded, involute lobe; antheridia solitary, the stalk uniseriate throughout or with 1-2 very local biseriate areas.

Gynoecia on main axis or on short to long lateral- or ventral-intercalary branches; subfloral innovations absent, but occasionally with a branch below bract or bracteole of first series; bracts in 3 series, those of innermost series plane to slightly concave, ovate to obovate to wide-elliptic, plane or undulate; apices undivided, broadly rounded to truncate, entire or sparingly dentate to laciniate, occasionally short-bifid, and then with lobes occasionally apiculate; lamina margins occasionally recurved, entire or with a few teeth. Bracteoles of innermost series free from bracts, *concave to canaliculate* (ventral view), *often appressed to the infolded ventral lobe of perianth*, rarely reflexed, the bracteoles orbicular to ovate to elliptic to obovate to subrectangular; apices undivided and truncate or bifid to 0.25; lamina margins entire or with a few teeth or 1 lobe. *Perianth strongly trigonous, subclavate to subcampanulate to elongate-subrectangular*, the *ventral side usually strongly infolded* and lending perianth ± bilaterally compressed, the *perianth sides straight or gradually expanding toward the ± bilaterally compressed wide mouth;* lobes commonly undulate, broadly rounded, *often flaring* and then broadly rounded to auriculate just distal to keel, the lobes entire, occasionally repand, occasionally regularly dentate to ciliate to laciniate; keels often with wings of a few to several cells high, the wings occasionally sparingly dentate.

Seta 8-19 cells in diameter, with *30-70 rows of outer cells* with walls moderate to very thick, with occasional intermediate thickenings, the inner corners with thickenings similar to large to bulging trigones; inner core of cells scattered, ca. equal to or slightly larger than outer row, thin-walled, with thickenings similar to small to large trigones. Capsule broadly ovate to elliptic, the valves 0.84-1.5 mm. long, 36-60 μ thick, of 4-6

Opposite:

FIG. 22. *Clasmatocolea humilis* (Hook. f. & Tayl.) Grolle. **1,** Main axis, lateral view of C. **humilis** var. **suspecta**; note leaf dentition. **2,** Leaves. **3,** Underleaves, showing major different shapes. **4,** Perianth mouth, ventral lobe in middle. **5,** Main axis, dorsal view of **hygrophilous form**; leaves removed to show leaf insertion and underleaf form. **6,** Main axis, ventral-lateral view of **hygrophilous form**. Figure 1, from *Engel 5010*, Chile, Prov. Magallanes, Pto. Alert; figure 2a, from *Dusén 360*, Chile, Prov. Chiloé, I. Guaitecas; figures 2b, 3a, b, from syntype of *C. humilis*, *Hooker*, Kerguelen (S); figure 3c, from *Dusén 66*, Chile, Prov. Valdivia, Corral; figure 3d, from *Dusén 38*, Chile, Prov. Magallanes, Pto. Bueno; figures 3c, d, from *Engel 5489*, Chile, Prov. Magallanes, F. Peel; figure 3e, from *Dusén*, Chile, Prov. Aisén, R. Aisén Valley; figure 3f, from *Dusén 360*, Chile, Prov. Chiloé, I. Guaitecas; figure 3g, from *Dusén 250*, Chile, Prov. Magallanes, Pto. Angosto; figure 3h, from type of *L. magellanica*, *Naumann*, Chile, Prov. Magallanes, B. Tuesday; figure 3i, from *Halle 222*, Argentina, Terr. Tierra del Fuego, L. Fagnano; figure 4, from *Engel 5483C*, Chile, Prov. Magallanes, F. Peel; figures 5, 6, from *Engel 5771B*, Chile, Prov. Magallanes, B. Tuesday.

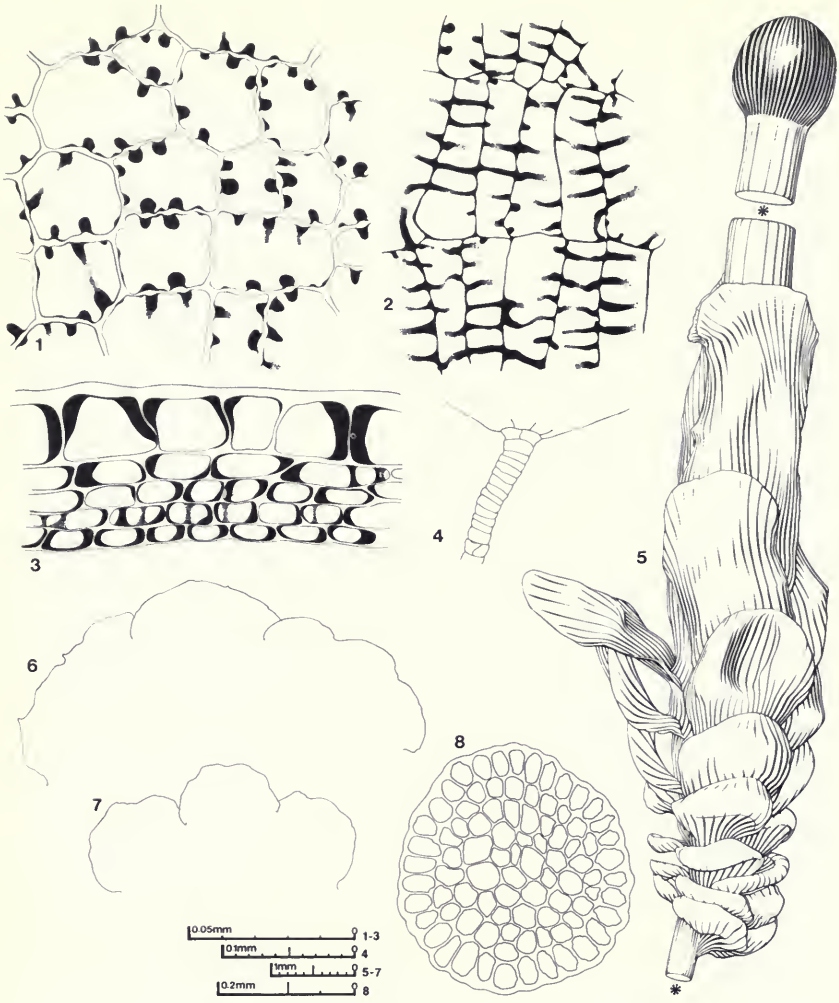


FIG. 23. *Clasmatocolea humilis* (Hook. f. & Tayl.) Grolle. **1,** Outer capsule wall cells. **2,** Inner capsule wall cells. **3,** Capsule wall, cross section. **4,** Antheridial stalk. **5,** Sporophyte bearing axis. **6, 7,** Perianth mouths, ventral lobes in middle. **8,** Seta, cross section. Figures 1, 2, 8, from *Engel 6299*, Chile, Prov. Magallanes, B. Pond; figure 3, from *Engel 4042B*, Chile, Prov. Osorno, near L. Toro; figure 4, from *Engel 4728*, Chile, Prov. Magallanes, I. Grant; figure 5, from *Engel 5472*, Chile, Prov. Magallanes, F. Peel; figure 6, from *Engel 2331*, Chile, Prov. Magallanes, Pto. Cutter; figure 7, from *Engel 3319*, Falkland Is., Weddell I., Waterfall Valley.

FIG. 24. *Clasmatocolea humilis* (Hook. f. & Tayl.) Grolle (includes all varieties).

layers; outer row of cells 18-23 μ thick, equal to thickness of 2.5-3 of interior strata; outer layer with vinaceous or red-brown, nodule-like to ± spinelike thickenings that are often feebly tangentially dilated, *semiannular bands absent;* exposed wall of outer layer thickened; intermediate and inner layers of cells subequal in thickness, the intermediate layers with thickenings often feebly extending onto tangential walls; inner layer of cells 4-6 μ thick, with red-brown semiannular bands, the bands often incomplete, the radial walls with nodulose thickenings often present.

Spores 10-15 μ, light brown, exine with the light microscope appearing minutely punctate, but under the SEM with densely granulate to short, wide vermiform projections covered with crowded, sometimes coalescing nanogranules, the intervening hollows with nanogranules; spores *averaging 1.2 × elater diameter.* Elaters 9-12 μ wide, apical portions often with thick nonspiral walls; elater walls light brown, 2 μ in diameter.

KEY TO VARIETIES OF *Clasmatocolea humilis*

1. Underleaves polymorphic in shape on any given axis, the apices usually undivided,

sporadically short-bifid; underleaves uniformly small for plant size, those in apical portion (0.8-)1.0-1.3 × stem width. Endemic to Tristan da Cunha..var. *polymorpha*

1. Underleaves ± consistent in shape on any given axis, the apices undivided or (frequently) bifid; underleaves not uniformly small for plant size, 1.0-4.3 × stem width.....2

2. Axes with leaves entire; perianth lobes entire or occasionally sparingly dentate var. *humilis*

2. Axes with at least some of leaves sparingly to regularly dentate; perianth lobes regularly dentate to ciliate to laciniate.....var. *suspecta*

Clasmatocolea humilis (Hook. f. & Tayl.) Grolle, var. **humilis.**

Jungermannia humilis Hook. f. & Tayl. London J. Bot. 3:468. 1844 *non J. humilis* Kash. & Chopra, Liverworts of the Western Himalaya and the Panjab Plains 2:88. *pl. 25, f. 5-7.* 1932 (= *?Jungermannia* sp.). *Mylia humilis* (Hook. f. & Tayl.) Trev. Mem. Ist. Lomb. Sci. Lett. III. 4:412. 1877. *Solenostoma humilis* (Hook. f. & Tayl.) Mitt. Philos. Trans. 168 (extra vol.):42. 1879. *Nardia humilis* (Hook. f. & Tayl.) Berggr. New Zealand Hep. 7. 1898. *Lophocolea humilis* (Hook. f. & Tayl.) Steph. Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26 (III, 6):40. 1900. *Leioscyphus humilis* (Hook. f. & Tayl.) Pears. Bull. Misc. Inform. 1922:249. 1922. *Clasmatocolea humilis* (Hook. f. & Tayl.) Grolle, Rev. Bryol. Lichénol. 29:72. 1960. Lectotype (*nov.*): Kerguelen, *Hooker s.n.* (FH!).

Jungermannia palustris Hook. f. & Tayl. London J. Bot. 3:464. 1844, *syn. fide* Engel (1978). *Lophocolea palustris* (Hook. f. & Tayl.) Besch. & Mass. Mission Sci. Cap Horn 5:222. 1889. Original material: Chile, Prov. Magallanes, I. Hermite, *Hooker 19b* (FH!, NY!, S!).

Lophocolea magellanica Schiffn. *in* Naumann, Forschungsr. *Gazelle* 4 (4):14, *pl. 4, f. 22, 23.* 1890, *syn. fide* Engel (1978). Holotype: Chile, Prov. Magallanes, I. Desolación, B. Tuesday, 2 February 1876, *Naumann s.n.* (FH! — c. per.).

Lophocolea hastatistipa Steph. K. Svenska Vetenskapsakad. Handl. 46 (9):45. *f. 19 h, i.* 1911, *syn. fide* Engel (1978). Lectotype (*fide* Engel, 1978): Falkland Is., King George B., 22 November 1907, *Halle & Skottsberg 352* (UPS!).

Lophocolea incrassata Steph. K. Svenska Vetenskapsakad. Handl. 46 (9):46. *f. 17 c, d.* 1911, *syn. fide* Engel (1978). Lectotype (*fide* Engel, 1978): Falkland Is., 1908, *Skottsberg 644* (G!).

Lophocolea integerrima Steph. K. Svenska Vetenskapsakad. Handl. 46 (9):46. *f. 17 a, b.* 1911, *syn. fide* Engel (1978). Lectotype (*fide* Engel, 1978): Chile, Prov. Magallanes, S. Skyring, F. de los Ventisqueros, 26 April 1908, *Halle & Skottsberg 211* (UPS! — c. per.).

Lophocolea rotundifolia Steph. K. Svenska Vetenskapsakad. Handl. 46 (9):52. *f. 19 r, s.* 1911, *syn. fide* Engel (1978). Lectotype (*fide* Engel, 1978): Chile, Prov. Magallanes, I. Atalaya, 25 May 1908, *Skottsberg 230* (UPS!).

Lophocolea catenulata Herz. Darwiniana 11:215. *f. 2.* 1957, *syn. nov.* Holotype: Argentina, Río Negro, Parque Nac. Nahuel Huapí, M. Tronador, 1500 m., 6 January 1937, *Donat 182* (JE!).

Axes with leaves entire. Perianth lobes entire or occasionally sparingly dentate.

Variation.—This species exhibits considerable variablity, and I am recognizing the following ecological variants:

Hygrophilous forms.—Plants lax, occasionally quite flaccid in texture; leaves erect, closely imbricate; plants frequently growing in or near water.

In extreme hygrophilous forms, the plants are comparatively large, delicate, and often quite flaccid in texture. The underleaves are loosely to closely inbricate, rather deeply convex (ventral view) and with margins curved dorsally to strongly incurved; the apices are undivided to retuse. Examples of this extreme condition are *Engel 2198*, *5373*, *5748*, *5769*, *5771B*, *5869*, *6052A*, and *6447* (see fig. 22), as well as syntype plants of *Jungermannia palustris*.

In the syntypes of *Jungermannia palustris*, which are quite flaccid in texture, the ventral portion of the leaf is deeply adaxially concave with the ventral margin incurved, whereas the dorsal portion of the leaf is concave, often with the dorsal margin decurved. This condition produces, in the leaf middle, the "remarkable longitudinal obtuse fold," noted in Hooker & Taylor (1844). There is a trend in variation toward this condition commencing in the more xeric forms of *C. humilis* with the ventral margin only slightly incurved and the dorsal portion of the leaf slightly concave. The trend then continues in aquatic forms, especially in the very flaccid plants, to the condition found in the syntypes of *J. palustris*. *Jungermannia palustris* is a good example of the hygrophilous facies of *C. humilis*.

Xerophilous forms.—Plants very rigid, stiff, never flaccid in texture; leaves spreading, more loosely imbricate; plants growing on rocks and in comparatively dry, exposed habitats.

The underleaves of *C. humilis* exhibit considerable variation. They may be plane to very slightly convex (ventral view) as in the type plants of *Jungermannia humilis*, to ± cucullate as in type plants of *Lophocolea magellanica*. They are orbicular to oblate to ovate to elliptic to subrectangular in shape. In undivided underleaves, the apex may be very wide

truncate or the underleaf may taper gradually to a narrowly rounded apex; in the latter instance the underleaf margins occasionally are incurved (dorsal view). Further, apices vary from unlobed (and broadly rounded or truncate) to retuse to bifid to varying degrees, but not to greater than 0.35. The unlobed apices may be entire or bidentate. It is not unusual to observe considerable variation in underleaf apices on a single axis. Underleaf margins are entire or with 1 slime papilla or with one tooth or lobe in the middle third, but may be dentate or small to large lobate in either upper, middle, or lower third of the underleaf margin. Some of this diversity in underleaf shape and armature is shown in Figure 22-3.

Differentiation.—Clasmatocolea humilis is related to *C. fasciculata;* see under the latter for distinguishing characters.

Clasmatocolea humilis should be separated with care from those phenotypes of *Lophocolea austrigena* with leaves concave (but never conchiform concave) and underleaves occasionally plane. The following ensemble of characters of *L. austrigena* will distinguish these plants: (a) underleaves universally connate on one side; (b) underleaf apices entire to bidentate to retuse; (c) underleaves occasionally strongly concave (recurved); and (d) leaves sporadically weakly to rather strongly convex. Character (c) sometimes is particularly evident toward axis apices.

In Australasia, care should be taken with certain facies of *Lophocolea gunniana* that have sporadically convex (ventral view) underleaves and adaxially concave leaves. Such plants are presumably an aquatic phase, and confusion with *C. humilis* is very possible. In this case characters (a), (c), and (d) listed above for *L. austrigena* also apply to *L. gunniana* and may also be used to distinguish the latter from *C. humilis.* See also the comments under *C. notophylla.*

I am including a discussion of *Lophocolea otiphylla* here because this species, when of certain facies, will key to Sect. *Clasmatocolea*, and within this group, it exhibits some relationship to *C. humilis.*

Lophocolea otiphylla has leaves that vary from distinctly convex to plane to very slightly concave (with the slight concavity restricted to the ventral-basal subauriculate portion of the leaf, which extends ventrally beyond the stem) to distinctly concave. These differences are largely dependent upon the orientation of the apex and ventral margin and not upon any natural tendency for concavity in the ventral-basal portion of the leaf lamina. Rather, the degree of concavity is correlated with the degree the apex and ventral margin are inflexed. On the other hand, the apex and both dorsal and ventral margins are occasionally all *reflexed,* and in this situation, the leaves are distinctly convex, lending a definite

Lophocoleoid appearance to the plants. When the leaves are convex, the plants, in general aspect, look quite like *L. austrigena* or *L. elata*, but certainly not like any *Clasmatocolea*.

This species, as mentioned above, shows some relationships to *C. humilis* and bears a rather striking resemblance to hygrophilous forms of that species, sharing such features as size, texture, and color of plants as well as form and size of underleaves. Examples of the hygrophilous form of *C. humilis* are syntype plants of *Jungermannia palustris* (= *C. humilis*). It is of interest that Hooker & Taylor (1844, p. 466) alluded to this connection when stating that their *Jungermannia otiphylla* "approaches our *Jungermannia palustris* from the same country and from similar situations."

Two features of *L. otiphylla* necessitate, in my mind, placement in *Lophocolea*, rather than *Clasmatocolea*. First, the leaves are frequently plane or distinctly convex, and then totally unlike any *Clasmatocolea* taxon, the leaves never have the distinct conchiform concavity so typical of many of the species of *Clasmatocolea*. Second, the androecial bracts of *L. otiphylla* are not strongly saccate at the base, but rather consist of a small, inflated lobule of minimal proportion to overall bract size and a lobe not much different from leaves. The bracts are thus quite leaflike and hardly spicate. In my experience with the genus *Lophocolea*, the male bracts tend to be more leaflike and nonspicate, very much like that of *L. otiphylla*. In *Clasmatocolea*, male bracts are either strongly saccate throughout or distinctly saccate in the basal portion, with the distal portion strongly concave. Further, the lobule is quite large in proportion to bract size, and the lobe is clearly differentiated from leaves.

Notes.—1. There has been some confusion surrounding the names *Solenostoma humilis* and *Nardia humilis*. Hooker & Taylor (1844) described *Jungermannia humilis* for a Kerguelen plant with well-developed underleaves, and the plate in Taylor & Hooker (1847) clearly indicates the presence of such structures. Mitten (1879) however, transferred the species to *Solenostoma* and stated (p. 42), "Both *S. humilis* and *J. inundata* were originally described as stipulate species, no amphigastria have, however, been since found on the specimens. It is probable that the figure of the supposed stipule of *J. humilis* may have been drawn from a fragment of *Leioscyphus turgescens*." Berggren (1898), in his treatment of New Zealand hepatics, believed his plants must be identical to those treated by Mitten (*loc. cit.*) but transferred the epithet to *Nardia*.

Stephani (1901) alleviated some of the confusion by stating he had seen original material of *Jungermannia humilis* that indeed possessed conspicuous underleaves and belonged to the genus *Lophocolea*. Stephani (*loc. cit.*), however, still used the name *Solenostoma humilis* for New

Zealand plants. Hodgson (1946) includes a discussion of this confusion.

All observed Berggren collections labeled *Solenostoma humilis* or *Nardia humilis* from various localities in North and South Islands, New Zealand, are *Jungermannia inundata* Hook. f. & Tayl. (15 specimens from LD and 11 from S).

2. *Lophocolea magellanica* is here regarded as a new synonym of *Clasmatocolea humilis*. When considering the spectrum of underleaf variation in *C. humilis*, the underleaves of type plants of *L. magellanica* exhibit an extreme form. The underleaves are rather deeply convex (ventral view), nearly orbicular in shape, and with apices truncate or shallowly and very broadly lunate. The underleaf apices may or may not be bidentate. The trigones of the type plants of *L. magellanica* are very large and bulging, and the perianth mouth entire, both characters of which are found within the variation of *C. humilis*.

3. The underleaves of *Lophocolea hastatistipa* are mostly bifid to 0.5 and with a large lobe on one or both sides of the underleaf base. The underleaves, however, may be entire or 1-dentate at the base and occasionally are lobate on one side and entire on the other. *Lophocolea hastatistipa* fits well within the variation circumscribed for *C. humilis* and is here reduced to synonymy.

4. The underleaves of *Lophocolea integerrima* are occasionally undivided, but more often bidentate with teeth of one to a few cells, or emarginate, or at most retuse. If bidentate or entire, the underleaf apices are then ± truncate. The underleaf margins are entire. Stephani (1911) states the plants of *L. integerrima* are sterile. However, upon examination of plants of syntype material, perianths were found to be present. *Lophocolea integerrima* fits well within the variation pattern of *C. humilis* and is here reduced to synonymy.

5. The syntypes of *Lophocolea rotundifolia* from "Azopardo-Tal" are misdeterminations of *Pachyglossa spegazziniana*. Of the remaining syntypes, the specimen from Isla Atalaya best fits the description and figures in Stephani (1911) and is here designated the lectotype.

6. The Gasperi collections of *Lophocolea magellanica* cited in Gola (1923) are actually specimens of *Pachyglossa spegazziniana* var. *spegazziniana* (*fide* specimens in FI!).

Ecology.—This variety has a somewhat wide ecological amplitude. In forests on the floor, over rocks, cliffs, and rotted logs. Rather frequently associated with streams—often on boulders, sometimes on logs over streams. The variety also occurs in moorland areas where over rock (mixed with *Lophocolea sabuletorum*) or in small pools.

The hygrophilous form seems to be restricted to cold, very high rainfall areas. On Isla Desolación, in western Tierra del Fuego, it occurred in pools of moorland areas on ridges and there commonly associated with *Isoetes* sp. It also occurs submerged in small lakes in the Patagonian Channel region.

Phytogeography.—Macquarie Is.; New Zealand, South I. (915 m.); Antipodes; Australia, New South Wales (2,000-2,300 m.); Kerguelen; Crozet Is.; Marion I. (15-130 m.); Prince Edward Is. (100 m.); Tristan da Cunha Group, Gough I. (170-505 m.), Tristan da Cunha (170-650 m.); Falkland Is. (sea level-595 m.); Tierra del Fuego (200-580 m.); Patagonian Channels; Valdivian region (100-1,240 m.; N. to 36° 43′ S.; and Andean Patagonia in Parque Nac. Nahuel Haupí) (see fig. 24).

Specimens seen.—**MACQUARIE IS.:** *Ashton 1112* as *C. crassiretis* (hb. Grolle); ibid., *Evans 6* (hb. Grolle). **NEW ZEALAND. SOUTH ISLAND.** SOUTHLAND: Fiordland Natl. Park, head of Hollyford Valley, near S. entrance to Homer Tunnel, Milford Rd., ca. 915 m., *Schuster 55596a* — c. ♂ (hb. Schuster). NELSON: Nelson Lakes Natl. Park, Travers Saddle, *Simpson 3412 p.p.* as *C. strongylophylla* (CHR). **ANTIPODES:** Hut Cove, *Godley s.n.* as *Lophocolea austrigena* (CHR); ibid., *Godley s.n.* as *C. paucistipula* (CHR). **AUSTRALIA.** NEW SOUTH WALES: Carruthers P., 2,000-2,300 m., *McVean 26449* — c. ♂, *26450* (hb. Grolle). **KERGUELEN:** *Sin. loc.*, *Hooker s.n.* as syntype of *J. humilis* (L, LD, S — c. ♂); Royal Sound, *Eaton s.n.* as *Leioscyphus turgescens* (BM, NY); ibid., *Eaton s.n.* (hb. Grolle); I. Longue, on margin of lake E. of le Kiosque (W. of Port-Bizet), 125 m., *Engel 8028A* (MSC). **CROZET IS.:** 1929, *sin. coll.* (S); I. de l'Est, *Hebrard 39B2* (hb. Grolle); ibid., *Ring & Raknes 69* (O). **MARION I.:** *Sin. loc.*, *Rand 3305* — c. per., *3394* (hb. Grolle); ibid., *Huntley 171*, *251k*, *255*, *942c* (PRE); ibid., *Huntley 945e* (hb. Grolle); Tarn Valley, 130 m., *Huntley 477* (F, hb. Grolle, PRE); Nellie Humps, *Bakker 207/b* (hb. Grolle); near weather station laboratory, 15 m., *Bakker 236/b* (hb. Grolle). **PRINCE EDWARD IS.:** Albatross Valley, 100 m., *Bakker 619h* (hb. Grolle, PRE). **TRISTAN DA CUNHA:** 600 m., *Christophersen & Mejland 984* — c. per. (O); S. of Round Hill, 650 m., *Christophersen s.n.* (UPS). **GOUGH I.:** Upper Watersmeet, 170 m., *Wace 539* as *L. diversistipa* (UPS); W. slopes of Gonydale, 505 m., *Wace 598a* (UPS). **FALKLAND IS.** (selected). **EAST FALKLANDS:** Port Stanley, *sin. coll.* (BM); ibid., *Halle s.n.* as *Lophocolea otiphylla* (UPS); ibid., *Halle 222* as *L. otiphylla* (NY, S); ibid., *Lechler s.n.* as *L. puccioana* (S); ibid., (*Lechler*) (FH, hb. Váňa); ibid., *Skottsberg s.n.* as *L. otiphylla* (UPS); ibid., Sapper Hill, *Skottsberg s.n.* as *L. otiphylla* (UPS); ibid., *Skottsberg 217* as *L. magellanica* (NY); ibid., *Skottsberg 222* as *L.*

otiphylla (NY, S); Port Harriet, *Halle s.n.* as *L. otiphylla* (UPS); ibid., *Halle 222* as *L. otiphylla* (NY, S); headwaters of Mullet Cr., *Engel 3161B*, *3167*, *3182* (MSC); Mt. Usborne, *Halle s.n.*, *230* as syntype of *L. rotundifolia* (UPS). **WEST FALKLANDS:** Hornby Mts., *Skottsberg 222* as *L. otiphylla* (S, UPS — c. ♂); Mt. Adam, basin E. of summit, 580-595 m., *Engel 2996A* — c. per., *2998A*, *3000* (MSC); Weddell I., *Halle & Skottsberg 226* as *L. puccioana* (S). **ARGENTINA.** TERR. TIERRA DEL FUEGO: R. Olivia, Ushuaia, *Skottsberg 231* as syntype of *L. skottsbergii* (LD, S); I. de los Estados, *Skottsberg s.n.* as *L. navistipula* (G, S); ibid., *Spegazzini s.n.* as *Leioscyphus turgescens* (NY); ibid., Pto. Cook, *Skottsberg s.n.*, *45* as *L. austrigena* (S); I. de los Estados, Pto. San Juan del Salvamiento, *Spegazzini 18*[3] as *Chiloscyphus notophyllus* (NY); E. of M. Olivia, Sa. de Sorondo, 580 m., *Crow 1846*, *1850* (MSC); S. side of Paso Garibaldi, along Ruta Nac. No. 3, 400 m., *Crow 1769* (MSC); Sa. Alvear, 380 m., *Roivainen 854c* (H); ibid., 370 m., *Roivainen 874* (F, H). **ARGENTINA/CHILE:** L. Fagnano, *Halle & Skottsberg 205* as *Lophocolea gottschaeoides* (S); ibid., *Halle 222* as *L. otiphylla* (S, UPS). **CHILE.** PROV. MAGALLANES: I. Saddle, *sin. coll. 167* as *L. palustris* (PC); I. Hoste, *sin. coll. 906* as *L. otiphylla* (PC); ibid., *Hyades s.n.* as *L. palustris* (FH); I. Londonderry, *Exped. Aust. Belgica s.n.* as *L. palustris* (FH); S. Skyring, Cabo Leon, *Hatcher 34-5* (F, UW-M); R. Fontaine, *Halle & Skottsberg 4* as *L. otiphylla* (S); ibid., *Halle & Skottsberg 222* as *L. otiphylla* (NY); R. Azopardo, *Dusén s.n.*, *169* (S); ibid., *Dusén 38* as *Lophocolea triseriata* (UPS); ibid., *Dusén 41*, *42* as *L. otiphylla* (S); ibid., *Dusén 56* (L, S, UPS); ibid., *Dusén 60* as *L. puccioana* (S); ibid., *Dusén 117* as *L. cookiana* (NY); I. Clarence, *sin. coll. 64* as *L. puccioana* — c. per. + ♂ (PC); ibid., "S. Hoss," *Hariot 64* as *L. puccioana* (PC); I. Clarence, B. Pond, *Engel 6291* — c. per., *6293* — c. per., *6298*, *6299* — c. sporo. (MSC); S. Otway, Pto. Pomar, *Halle & Skottsberg 225* as syntype of *Lophocolea patulistipa* (UPS); I. Desolación, *Dusén s.n.* as *L. magellanica* (FH); ibid., *Dusén s.n.* (S); ibid., *Dusén* as *L. puccioana* (NY, S); ibid., Pto. Angosto, *Dusén s.n.* (S); ibid., *Dusén 169* (LD, NY, S); ibid., *Dusén 172* as *L. otiphylla* — c. per. (S); ibid., *Dusén 176*, *225*, *249*, *252*, *371* (UPS); ibid., *Dusén 250* (JE, L, S, UPS); ibid., *Dusén 268* as *L. gayana* (S); ibid., *Dusén 373* as *L. puccioana* (S); ibid., ca. 200 m., *Dusén 180* (S); ibid., *Dusén 384* as *L. puccioana* (NY, S); Pto. Angosto, *Dusén s.n.* (LD); I. Desolación, Pto. Churruca, head of Br. Lobo, *Engel 5822B*, *5869* (*hygrophilous fo.*) (MSC); I. Desolación, B. Tuesday, head of inner harbor, *Engel 5691*, *5708*, *5748* — c. ♂ (*hygrophilous fo.*), *5769* (*hygrophilous fo.*), *5771B* (*hygrophilous fo.*) (MSC); Brunswick Pen. (cf. Engel, 1978); E. side of B. Borja, *Engel 6122* — c. sporo. (MSC); S. Skyring, F. de Los Ventisqueros, *Halle & Skottsberg 222* as *L. otiphylla* (NY, S, UPS); S. Skyring, B. Pinto, *Halle &*

Skottsberg 222 as *L. otiphylla* (UPS); I. Pacheco, Pto. Ramon, *Skottsberg 144* as *Jamesoniella oenops* (UPS); Can. Smyth, Pto. Ramirez, *Skottsberg 198* as syntype of *L. diversistipa* (LD, S, UPS); I. Newton, *Dusén 56* (NY); ibid., *Dusén 117* as *L. puccioana* (NY); Pto. Bueno, *Dusén 38* as *L. otiphylla* (S); ibid., *Dusén 42* as *L. otiphylla* (NY); ibid., *Dusén 49* as *L. puccioana* (FH, NY); ibid., *Dusén 50* as *L. puccioana* (JE); ibid., *Dusén 103* (NY); head of F. Peel, *Engel 5472* — c. sporo., *5489* (MSC); F. Peel, *Skottsberg 222* as *L. otiphylla* (UPS); ibid., N. shore of Cta. Amalia, *Engel 5384* — c. sporo., *5423* — c. per. (MSC); Can. Messier, Cta. Rayo, *Skottsberg 225* as syntype of *L. patulistipa* (S); ibid., *Skottsberg 230* as syntype of *L. rotundifolia* (UPS); E. side of I. Juan, *Engel 5373* (*hygrophilous fo.*) (MSC); S. side of I. Madre de Dios, head of fiord E. of M. Roberto, *Engel 5129A*, *5157* (MSC); Pto. Charrúa, E. of Pta. Brown, *Engel 4590A*, *4596* — c. per. + ♂ (MSC); ibid., main cove S. of Pta. Brown, *Engel 4633C*, *4649A* — c. ♂, *4651* (MSC); Pto. Alert, head of fiord W. of M. Markham, *Engel 4976* (MSC); B. Halt, *Lechler s.n.* (BM). PROV. AISÉN: Pto. Island, *Engel 4338A* (MSC); B. Chacabuco, *Halle 220* as *L. navistipula* (BM, LD, S, UPS); ibid., *Halle 226* as *L. puccioana* (S); R. Aisén, *Dusén s.n.* (BM, JE, LD, S); ibid., *Dusén 222* as *L. puccioana* (NY); ibid., *Dusén 249* (FH); ibid., *Dusén 250* — c. per. (NY); ibid., *Dusén 949* — c. per. (O); Pro. Puyuhuapi, *Schwabe 43* as *L. otiphylla* (S); ibid., L. Risopatron, *sin. coll. 22* (JE); C. Tesoro, *Schwabe 39a* as *L. rotundifolia* (JE); ibid., 960-1,000 m., *Schwabe 39b*, *39/c p.p.*, *40 p.p.* as *L. rotundifolia* (JE). PROV. CHILOÉ: I. Guaitecas, *Dusén s.n.* (hb. Grolle, JE, LD, S); ibid., *Dusén s.n.* as *L. puccioana* (NY); ibid., *Dusén 24* as *L. puccioana* (S); ibid., *Dusén 360* (FH, NY, S); ibid., Bo. Chica, *Dusén s.n.* as *L. puccioana* (JE); ibid., *Dusén 375* as *L. otiphylla* — c. per. (NY); ibid., *Dusén 384* as *L. puccioana* (NY); I. Guaitecas, Melinca, *Halle 210* (S); ibid., *Dusén 352* (NY); Melinca, *Dusén s.n.*, *?35a* (S); I. Guaitecas, Pto. Low, *Dusén s.n.*, *336* (S); M. Corcovada, *Halle & Skottsberg s.n.* as syntype of *L. rotundifolia* (UPS); ibid., *Skottsberg s.n.* as syntype of *L. rotundifolia* (G); I. Chiloé, Cord. San Pedro, near aserradero at San Pedro, R. Puidi, 320 m., *Engel 11914* — c. per. (F); I. Chiloé, Aguas Buenas area, 4.7 km. E. along Aguas Buenas road from Ancud-Quemchi road, ca. 100 m., *Engel 12189* — c. sporo. (F). PROV. LLANQUIHUE: L. Todos los Santos, Cayutue, *Wolffugel s.n.* as *L. rotundistipula* (JE). PROV. OSORNO: near L. Toro on road to Refugio Antillanca, 855 m., *Engel 3961B* (MSC); Agua Caliente, R. Chanleufú, 4 km. by road from Termas de Puyehue along road to Refugio Antillanca, 400 m., *Engel 11425*, *11437* (F); Termas de Puyehue, *Schwabe 63/d p.p.* as *L. rotundifolia* — c. ♂ (JE). PROV. VALDIVIA: L. Puyehue, *Mahu 7568* (JE, hb. Mahu); W. slope of Cord. Pelada, W. of El Mirador, between La Union and Pta. Hueicolla, 680-

840 m., *Engel 12333*, *12341* (F); Los Ulmos, *Mahu 7770* (hb. Grolle); R. Futa, *Schwabe 15* (JE); Corral, *Dusén 66* (S). PROV. CAUTÍN: Parque Nac. Conguillo, 1,110 m., *Mahu 10823* (hb. Mahu) PROV. MALLECO: Parque Nac. Nahuelbuta, *Mahu 6035* (JE, hb. Mahu). PROV. MALLECO/PROV. ARAUCO: Cord. Nahuelbuta, Parque Nac. Nahuelbuta, 48 km. W. of Angol, Aquas Calientes, 1,240 m. *Engel 12610* (F). PROV. CONCEPCIÓN: Talcahuano, *Dusén 72* as *L. otiphylla* — c. per. (NY); ibid., *Dusén 172* as *L. otiphylla* (S). **ARGENTINA.** PROV. RÍO NEGRO: Puerto Blest, *Dusén 504* (S). PROV. RÍO NEGRO/PROV. NEUQUÉN: L. Nahuel Huapí, *Dusén s.n.* as *L. puccioana* (FH). Patagonia: *Sin. loc.*, *Skottsberg s.n.* as syntype of *L. patulistipa* (G); ibid., *Skottsberg s.n.* as syntype of *L. integerrima* (G).

Clasmatocolea humilis var. **suspecta** (Mass.) Engel.

Lophocolea puccioana var. *β suspecta* Mass. Nuovo Giorn. Bot. Ital. I. 17:228. 1885. *Clasmatocolea humilis* var. *suspecta* (Mass.) Engel, Phytologia 41:309. 1979. Lectotype (*nov.*): Argentina, Terr. Tierra del Fuego, I. de los Estados, M. Conegliano, March 1882, *Spegazzini 170* (VER! — c. per. + ♂).

Lophocolea multispinula Steph. Spec. Hep. 6:284. 1922. Original material: Chile, Prov. Magallanes, I. Desolación, B. Tuesday, *sin. coll.* (G!).

Leioscyphus patagonicus Pears. Bull. Misc. Inform. Kew 1922:250. *1 pl.* 1922, *syn. nov.*, *non L. patagonicus* Steph. Kongl. Svenska Vetenskapsakad. Handl. 46 (9):38. 1911 (= *Leptoscyphus*). Holotype: Chile, Prov. Magallanes, S. Molyneux, 1 June 1896, *Dusén s.n.* (BM! — c. ♂; isotypes: BM! — c. ♂, hb. Grolle!).

Lophocolea hickenii Herz. Hedwigia 66:90. *f. 7.* 1926, *syn. nov.* Holotype: Chile, Prov. Aisén, B. San Rafael, 26 February 1921, *Hicken 68/a* (JE!).

Axes with at least some of leaves sparingly to regularly dentate, the leaves with up to 10 teeth. Perianth lobes regularly dentate to ciliate to laciniate.

Differentiation.—This variety differs from var. *humilis* by possessing leaves that are sparingly to regularly dentate. With regard to leaf armature, at one end of the continuum are plants in which a few leaves on a given axis have one or a few teeth, such as in syn- and lectotype plants of *Lophocolea puccioana* var. *β suspecta* and original material of *Leioscyphus patagonicus*. At the other extreme are plants in which the leaves are regularly and often coarsely dentate, such as holotype plants of *Lophocolea hickenii*, *Engel 4042B*, *4050C*, *12280*, and *12406*. There is a steady

continuum toward the development of this extreme and, interestingly, those phenotypes with dense, coarse teeth tend to be copiously branched and are very commonly corticolous. I have spent considerable time in assessing whether the copiously branched, coarsely toothed facies might better be treated as a discrete, if narrowly circumscribed, separate species. However, the "cut-off point" in the definition of such a species would be purely arbitrary, and I prefer to treat this complex as a rather plastic one—both morphologically and ecologically.

Confusion of this variety with *C. fulvella* is possible when *C. humilis* var. *suspecta* occasionally produces rather copious, short lateral-intercalary branches that are subvermiform or submoniliform and with branch underleaves more closely imbricate than in main axes. In such cases, *C. humilis* var. *suspecta* may be distinguished from *C. fulvella* by (a) main axis underleaves at most moderately convex (ventral view), with margins neither curved dorsally nor ± clasping the stem; and (b) intercalary branch underleaves usually short-bifid with segments conspicuously evident. *Clasmatocolea fulvella*, on the other hand, has (a) main axis underleaves cupulate, with margins curved dorsally and ± clasping the stem; and (b) intercalary branch underleaves usually undivided, distinctly cupulate and appearing inflated. This facies of *C. humilis* var. *suspecta* represents one kind of example of those phenotypes with coarse, dense teeth (see discussion above).

Note.—Stephani (1922) states for the leaves of *L. multispinula*, "ceterum ubique regulariter spinuosa," but was probably referring to leaves of the smaller branches, which are more regularly and consistently dentate than the leaves of the main axis or larger branches. The leaves of the latter are entire or sparingly to irregularly dentate. The type plants are rather small.

Ecology.—This variety seems to prefer well-shaded niches. In the Magellanian forests it occurs on *Berberis illicifolia*, etc., and in rocky stream valleys. In the Valdivian region it occurs in forests from near sea level to 840 m., and there on moist decorticated logs or on *Nothofagus* bark. This variety, compared to var. *humilis*, is more often corticolous.

Phytogeography.—Marion I.; Tristan da Cunha; South Georgia; Patagonian Channels; Valdivian region (N. to 39° 52′ S. in Prov. Valdivia; Andean Patagonia in Parque Nac. Nahuel Huapí); and on Mas a Tierra, Juan Fernández Is. (see fig. 24).

Specimens seen.—**MARION I.:** *Huntley 727* (F, JE, PRE); *Huntley 890/a* (F, PRE); *Huntley 937a* (PRE). **TRISTAN DA CUNHA:** 400 m., *Christophersen & Mejland 96* (O). **SOUTH GEORGIA:** Bay of Isles, Rosita Hr., *Skottsberg 222* (hb. Grolle). **ARGENTINA.** TERR. TIERRA

DEL FUEGO: I. de los Estados, "New Year Harbour," *Spegazzini 84* as syntype of *L. puccioana* var. *β. suspecta* — c. per. + ♂ (VER); ibid., M. Conegliano, Pto. Cook, *Spegazzini s.n.* as *L. puccioana* (NY). **CHILE.** PROV. MAGALLANES: I. Hermite, *Hariot 129* as *L. puccioana* var. *suspecta* (VER); Ens. Villarino, *Hatcher s.n.* as *L. puccioana* var. *suspecta* (FH, VER); I. Capitan Arecena ("I. Clarence"), Pto. Hope, S. Magdalena, *Spegazzini 234* as *L. puccioana* var. *β. suspecta* (VER); I. Desolación, *Dusén 263* as *L. fulvella* (S); ibid., Pto. Angosto, *Dusén 169* (UPS); ibid., *Dusén 250* (L, LD); ibid., *Dusén 268* as *L. gayana* — c. per. (NY); I. Desolación, Pto. Churruca, head of Br. Lobo, *Engel 5810* (MSC); I. Desolación, Pto. Churruca, N. side of Fo. Nassau, *Engel 5933A*, *5938D* (MSC); F. Peel, *Engel 5483C* — c. sporo. (MSC); Cta. Rayo, *Skottsberg 225* as syntype of *Lophocolea patulistipa* (UPS); I. Chatham, N. shore of B. Wide, *Engel 5304A* (MSC); S. side of I. Madre de Dios, head of fiord E. of M. Roberto, *Engel 5110* — c. sporo. (MSC); S. Molyneux, *Dusén s.n.* (S); Pto. Charrúa, *Engel 4823*, *4829* (MSC); Pto. Alert, *Engel 4897* — c. per., *5029* (MSC); ibid., head of fiord W. of M. Markham, *Engel 5005* — c. sporo., *5010* — c. sporo. (MSC). PROV. AISÉN: I. Magdalena, *Schwabe 20/e* as *L. puccioana* — c. per. + ♂ (JE); ibid., *Schwabe 20e-H* (JE). PROV. CHILOÉ: Pto. Ballena, *Engel 4197B* (MSC), I. Guaitecas, *Dusén 352* as *L. puccioana* (JE); ibid., Melinca, *Halle 210* (UPS); I. Guaitecas, Pto. Low, *Dusén s.n.* (JE); I. Chiloé, Pto. Quellon, *Halle s.n.* (hb. Grolle); ibid., *Halle 222* as *Lophocolea otiphylla* (UPS); I. Chiloé, Aguas Buenas area, 4.7 km. along Aguas Buenas road from Ancud-Quemchi road, ca. 100 m., *Engel 12190* (F). PROV. OSORNO: Antillanca, 700 m., *Ruthsatz 59/30* (hb. Grolle); around L. Toro on road to Refugio Antillanca, 855-885 m., *Engel 4025A*, *4042B* — c. sporo. + ♂, *4050C*, *4063A* — c. per. + ♂ (MSC); Agua Caliente, R. Chanleufú, 4 km. from Termas de Puyehue along road to Refugio Antillanca, 400 m., *Engel 11480* — c. ♂ (F). PROV. VALDIVIA: W. slope of Cord. Pelada W. of El Mirador, between La Union and Pta. Hueicolla, 580 m., *Engel 12280* (F); E. slope of Cord. Pelada, E. of El Mirador, between La Union and Pta. Hueicolla, 740-840 m., *Engel 12406*, *12418*, *12467* (F); R. Futa in vicinity of Futa, 5.9 km. by road S. of junction of highway T-60 and T-65, near sea level, *Engel 10810* (F); Corral, *Dusén 191* as *L. puccioana* (NY); ibid. [Quitaluto], *Hosseus 117* as *L. ctenophylla* (JE). **ARGENTINA.** PROV. RÍO NEGRO: Puerto Blest, *Dusén 304* (NY); ibid., *Dusén 504* (UPS). Patagonia: *Sin. loc.*, *Dusén s.n.* as *L. puccioana* — c. per. (FH). **JUAN FERNÁNDEZ IS.:** Mas a Tierra, Cordón del Barril, *Skottsberg 249* as *L. rotundifolia* (JE).

Clasmatocolea humilis var. **polymorpha** Engel.

Clasmatocolea humilis var. *polymorpha* Engel, Phytologia 41:309. 1979. Holotype: Tristan da Cunha, above settlement, 620 m., 21 December 1938, *Christophersen & Mejland 52* (O!; isotype: S!).

Leaves erect, often connivent, with margins and apices entire; underleaves on any given axis polymorphic: variable in shape and with apices often broadly rounded to truncate to retuse, and only sporadically short-bifid, often with one lobe well developed and the other represented as a tooth; underleaves distant, uniformly small for plant size, those in apical portion (0.8-)1.0-1.3 × stem width, the underleaves generally decreasing in size toward stem base, those toward stem base ca. 0.7 × stem width.

Ecology-Phytogeography.—Endemic to Tristan da Cunha, where over dripping rocks at 620-1,200 m. (see fig. 24).

Specimen seen.—**TRISTAN DA CUNHA:** Above Burntwood, 1,200 m., *Christopherson 774* (hb. Grolle).

Clasmatocolea fasciculata (Nees) Grolle. Figures 25-27.

Jungermannia fasciculata Nees, Hor. Phys. Berol. p. 46. *pl. 5, f. 4.* 1820 *non J. fasciculata* (Lindenb.) Hook. f. & Tayl. London J. Bot. 3:371. 1844 (= *Plagiochila*). *Chiloscyphus fasciculatus* (Nees) G. L. & N. Syn. Hep. 190. 1845. *Heteroscyphus fasciculatus* (Nees) Schiffn. Oesterr. Bot. *Z.* 60:172. 1910. *Lophocolea fasciculata* (Nees) S. Arnell & Grolle *in* Grolle, Trans. Brit. Bryol. Soc. 3:584. 1959. *Clasmatocolea fasciculata* (Nees) Grolle, Rev. Bryol. Lichénol. 29:72. 1960. Original material: South Africa, Cape Prov., Cape of Good Hope, *Ecklon* (W, Lindenberg Hep. No. 4501!).

Jungermannia bergiana Lehm. Nov. Minus Cogn. Stir. Pug. 4:43. 1832, *syn. fide* G. L. & N. (1845). Original material: South Africa, Cape Prov., Cape of Good Hope, *Bergius 29* (W, Lindenberg Hep. No. 4499! & 4500!).

Chiloscyphus fasciculatus var. β *dregeana* Nees *in* G. L. & N. Syn. Hep. 190. 1845, *syn. fide* Grolle (1959). *Jungermannia dregeana* Lehm. & Lindenb. *ex* G. L. & N. Syn. Hep. 190. 1845, *nom nud., pro syn.* Original material: South Africa, Cape Prov., Deutsch Kloof, 305-610 m., *Drege 1030* (W, Lindenberg Hep. No. 4497!).

Chiloscyphus fasciculatus var. γ *exarida* Nees *in* G. L. & N. Syn. Hep. 190. 1845, *syn. fide* Grolle (1959). Original material: South Africa, Cape Prov., summit of Table Mt., *Ecklon* (W, Lindenberg Hep. No. 4498!).

Chiloscyphus rabenhorstii Steph. Bull. Herb. Boissier 8 (1):51. 1908 (= Spec. Hep. 3:227), *syn. fide* Grolle (1959). *Heteroscyphus raben-*

FIG. 25. *Clasmatocolea fasciculata* (Nees) Grolle. **1,** Portion of main axis, dorsal view. **2,** Portion of main axis with ventral-intercalary (vib) and lateral-intercalary (lib) branches, lateral-ventral view. **3,** Underleaves of main axis (semiflattened). **4,** Leaves of main axis (semiflattened). **5,** Teeth of apices and margins of main axis leaves. Figures 1, 3a, e, 4a, b, from type of *C. fasciculata*, *Ecklon*, South Africa, Cape of Good Hope; figures 2, 3d, 4c, 5b, c, e, from *Esterhuysen 24164*, South Africa, Cape Prov., Waterfall Kloof; figures 3b, 4d, 5a, from type of *Chiloscyphus fasciculatus* var. *β dregeana*, *Drege*, Deutsch Kloof; figure 3c, from *Brunnthaler*, South Africa, Table Mt.; figure 3f, from *Esterhuysen 27356*, South Africa, P. Formosa; figure 3g, from *Drege 44*, South Africa, Cape of Good Hope; figures 4e, 5d, from *Esterhuysen 25380*, South Africa, Cape Prov., Kromrivierkloof; figure 5f, from *Esterhuysen 25128*, South Africa, Table Mt.

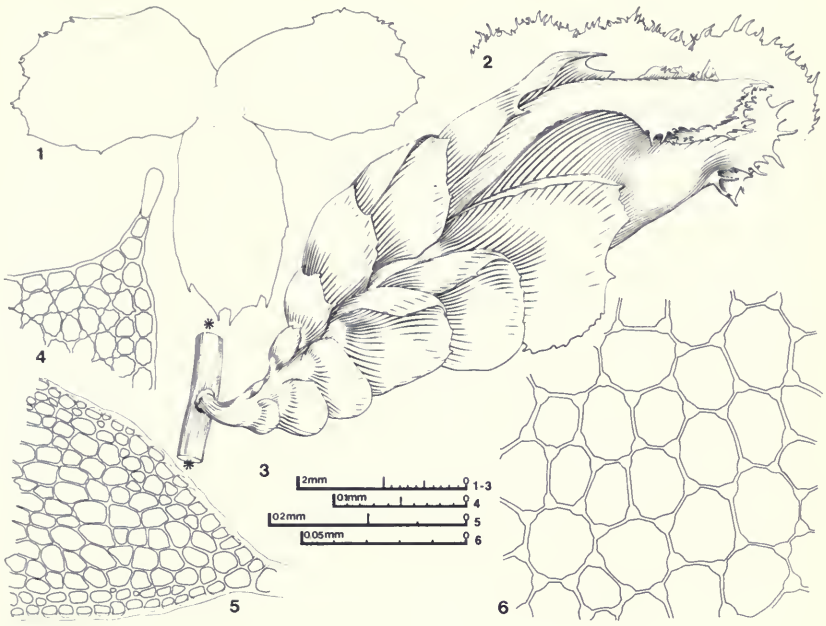


FIG. 26. *Clasmatocolea fasciculata* (Nees) Grolle. **1,** Bracts and bracteole. **2,** Perianth mouth. **3,** Gynoecium on ventral-intercalary branch; leaves and underleaves of main axis removed. **4,** Portion of main axis underleaf segment with a slime papilla. **5,** Stem, cross section. **6,** Median leaf cells. Figures 1, 2, after Grolle (1959); figure 3, adapted from Grolle (1959); figure 4, from type of *Chiloscyphus fasciculatus* var. *β dregeana*, *Drege*, Deutsch Kloof; figures 5, 6, from type of *C. fasciculata*, *Ecklon*, South Africa, Cape of Good Hope.

horstii (Steph.) Schiffn. Oesterr. Bot. *Z.* 60:172. 1910. Original material: South Africa, Cape Prov., Table Mt., February 1884, *Rabenhorst f.* (G!).

Lophocolea vermicularis Herz. Memoranda Soc. Fauna Fl. Fenn. 27:100. *f. 44 f-i.* 1952, *syn. fide* Grolle (1959). Holotype: South Africa, Cape Prov., Table Mt., ca. 600-800 m., 16 April 1922, *Rolfes 22* (JE!).

Isotachis capensis Steph. *ex* Herz. Memoranda Soc. Fauna Fl. Fenn. 27:101. *f. 45 a-f.* 1952, *syn. fide* Grolle (1959). Original material: South Africa, Cape Prov., Table Mt., *Rehmann s. n.* (JE, "A. Rehmann: Hepaticae austro-africanae. N°. 33a"!; Cape Prov., Table Mt., *Jelinek* (JE, "Exped. Novara"!); Cape Prov., *sin coll.* (with *Adelanthus unciformis*) (*non vidi*).

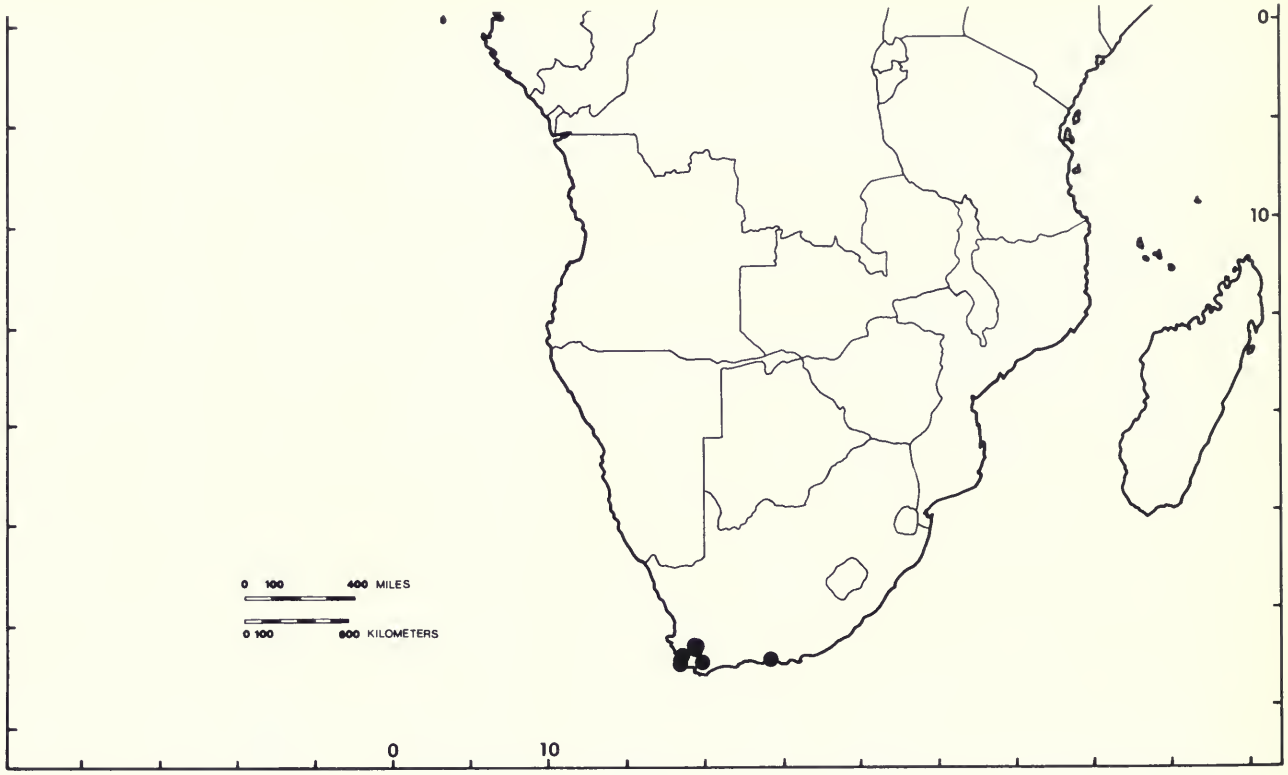


FIG. 27. *Clasmatocolea fasciculata* (Nees) Grolle.

Plants soft, spongy, prostrate, mixed with other bryophytes or densely caespitose, occasionally cushion-like, grey green, becoming brownish with age; *axes to* 4.7 cm. tall, *1.8 mm. wide* (to 2.5 mm. wide in axes with spreading leaves).

Branches frequent, occasionally in irregular fascicles, usually of lateral and ventral intercalary type, but Frullania-*type quite common*, rarely of *Acromastigum*-type; *branches usually with first 1-3 pairs of leaves bifid*, especially on intercalary branches.

Stems 11-15 cells high, cortex in 1-3 rows of moderately thick-walled cells smaller than medullary cells, the exposed wall of outer row moderately to very thickened; cuticle smooth; endophytic hyphae absent. Rhizoids, when present, in fascicles from stem near underleaf base.

Leaves with insertion very slightly to distinctly recurved at ventral end; leaves connivent dorsally, lending axis a somewhat vermiform appearance, occasionally rather strongly spreading or connivent in region of axis apices and spreading in region of axis base; leaves loosely-densely imbricate, conchiform concave, *wide-ovate to oblate to occasionally ± reniform;* apex broadly rounded to truncate to broadly retuse, undivided, occasionally inflexed, *the leaves entire or with a few teeth on apex or median-upper ventral margin, rarely dentate on dorsal margin; teeth wide-triangular and sometimes ± apiculate, or narrowly and often sharply triangular*, occasionally terminating in a unicellular row of several cells, the teeth commonly inflexed; dorsal margin plane to sinuous, short to long decurrent; ventral margin very often inflexed, broadly rounded, with basal portion enlarged, often extending ventrally beyond stem and in contact with slightly spreading underleaf.

Leaf cells thin walled, trigones large to bulging, rarely confluent; median leaf cells 16-26(-31) μ wide; 18-32 μ long; cuticle smooth.

Underleaves 2-3 × stem width, free, transversely or obliquely inserted, *approximate-imbricate, moderately to deeply convex, occasionally with basal portion abruptly convex (ventral view), the margins curved dorsally; underleaves reniform to wide-ovate to occasionally moderately ovate; apices 0.2-0.3-bifid*, the segments often apiculate, terminating in a slime papilla, segment margins entire or few dentate, with armature terminating in a slime papilla; *margins of the lamina usually with 1 large often apiculate lacinium variable in position, the margins otherwise entire or sparingly dentate-ciliate-laciniate.*

Plants apparently dioecious; androecia not seen.

Gynoecia on short ventral-intercalary branches; subfloral innovations absent; bracts in 2 series, those of innermost series oblong-obovate, apical portion often sharply inflexed or reflexed; apices broadly rounded to truncate to subretuse, entire or sparingly small-dentate; margins straight or reflexed, entire or with a few small teeth that often terminate in slime papillae. Bracteoles of innermost series free from bracts, slightly narrower than bracts, otherwise subequal to bract size, obovate; apices undivided or short-bifid; margins plane or sharply inflexed or reflexed, entire or sparingly small-dentate, the teeth often terminating in a slime papilla. *Perianth inflated, obscurely trigonous, wide-oblong, slightly narrowing toward a wide mouth;* lobes broadly rounded, often with portion of apex sharply reflexed, *the lobes with numerous sharp teeth-laciniae* that occasionally terminate in a slime papilla; keel wings occasional, of few cells high.

Sporophyte not seen.

Variation.—The type material of *C. fasciculata* possesses both connivent and rather strongly spreading leaves. This condition sometimes occurs on a single axis, and the leaves then are connivent in the region

of the axis apex and spreading in the area of the axis base (see fig. 25-1). Leaf armature of type plants is also variable—although many of the leaves are entire, there are usually at least several on a given axis with small to large, commonly inflexed teeth.

Differentiation.—I concur with Grolle (1959) that *C. fasciculata* is most closely allied to *C. humilis*. The following ensemble of features of *C. fasciculata* will serve to distinguish it from that species: (a) the laciniate underleaf lamina margins; (b) the restriction of perianths to short ventral-intercalary branches; (c) the perianths that slightly narrow toward a wide mouth, with the ventral lobes not infolded; and (e) the usually bifid initial 1-3 leaves of intercalary branches.

Note.—Clasmatocolea fasciculata produces, on rare occasion, *Acromastigum*-type branching. This, to my knowledge, is the first record of this branch type in the Lophocoleaceae. The plastic branching found in this species (ventral- and lateral-intercalary, *Frullania*- and *Acromastigum*-type branches) marks this taxon as a rather primitive element within the genus.

Ecology-Phytogeography.—On wet rock in streams and on damp, shaded south-facing slopes at altitudes of ca. 300-1,200 m. The species is endemic to Cape Prov., South Africa (see fig. 27).

Specimens seen.—**SOUTH AFRICA.** CAPE PROV.: "Kapland," *sin. coll.* — c. young per. (JE); Cape of Good Hope, *sin. coll.* (W); ibid., *Drege s.n., 44* (W); ibid., Tafelberg, ca. 900-1,000 m., *Brunnthaler s.n.* (hb. Grolle, W); Table Mt., upper Disa Gorge, 760 m., *Esterhuysen 25128* as *C. vermicularis* (UPS); Table Mt., NE corner of Holy Hutchinson Water Reservoir, *Arnell 892* as *I. capensis* (G); Betty's B., Porter Nature Reserve in kloof behind Botanic Garden, *Magill 6295* (F); Riviersonderend Reeks area, Riviersonderend, *Wilman 556* as *L. vermicularis* (BOL); Riviersonderend Reeks, Schilpadkop area, 760-915 m., *Esterhuysen 21102* as *L. vermicularis* (BOL); Waterfall Kloof, off Elandskloof, off Du Toitskloof, *Esterhuysen 24164* (BOL); Kromrivierkloof, off Du Toitskloof, *Esterhuysen 25380* (BOL); Witteberg, Slanghoekberge, 915 m., *Esterhuysen 22268* as *L. vermicularis* (BOL); Mostertshoek, 1,220 m., *Esterhuysen 24287* (BOL); foot of P. Formosa, *Esterhuysen 27356* as *L. vermicularis* (UPS).

Clasmatocolea vermicularis (Lehm.) Grolle. Figures 28-30, Plates 11, 12.

Jungermannia vermicularis Lehm. Linnaea 4:361. 1829 *non J. vermicularis* Hüb. Hepaticol. Germ. p. 187. 1834 [= *Lophozia sudetica* (Nees) Grolle]. *Alicularia vermicularis* (Lehm.) G. L. & N. Syn. Hep. 11. 1844. *Nardia vermicularis* (Lehm.) Trev. Mem. Ist. Lomb. Sci. Lett. III. 4:400. 1877. *Notoscyphus vermicularis* (Lehm.) Steph. Bull. Herb. Boissier 1 (2):174. 1901 (= Spec. Hep. 2:35). *Clasmatocolea*

vermicularis (Lehm.) Grolle, Rev. Bryol. Lichénol. 29:78. 1960. Original material: South Africa, Cape Prov., Table Mt., *Ecklon* (FH!, NY!, S!).

Jungermannia flexuosa Lehm. Linnaea 4:361. 1829, *syn. fide* Stephani (1901). *Alicularia flexuosa* (Lehm.) Nees *in* G. L. & N. Syn. Hep. 11. 1844. *Notoscyphus flexuosus* (Lehm.) Sim, S. African J. Sci. 12:20. 1916. Original material: South Africa, Cape Prov., Table Mt., *Ecklon* (G!).

Jungermannia subintegra Hook. f. & Tayl. London J. Bot. 3:477. 1844, *syn. fide* Grolle (1960). *Lejeunea subintegra* (Hook. f. & Tayl.) G. L. & N. Syn. Hep. 376. 1845. *Lophocolea subintegra* (Hook. f. & Tayl.) Grolle, Trans. Brit. Bryol. Soc. 3:587. 1959. Original material: Falkland Is., *Hooker* (FH!, NY!).

Jungermannia chamissonis Gott. & Lindenb. *in* G. L. & N. Syn. Hep. 668. 1847, *syn. fide* Grolle (1960). *Leptoscyphus chamissonis* (Gott. & Lindenb.) Mitt. Hooker's J. Bot. Kew Gard. Misc. 3:358. 1851. *Mylia chamissonis* (Gott. & Lindenb.) Trev. Mem. Ist. Lomb. Sci. Lett. III. 4:412. 1877. *Leioscyphus chamissonis* (Gott. & Lindenb.) Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15:445. 1885. Original material: Chile, without specific locality, *Chamisso* (S! — c. ♂).

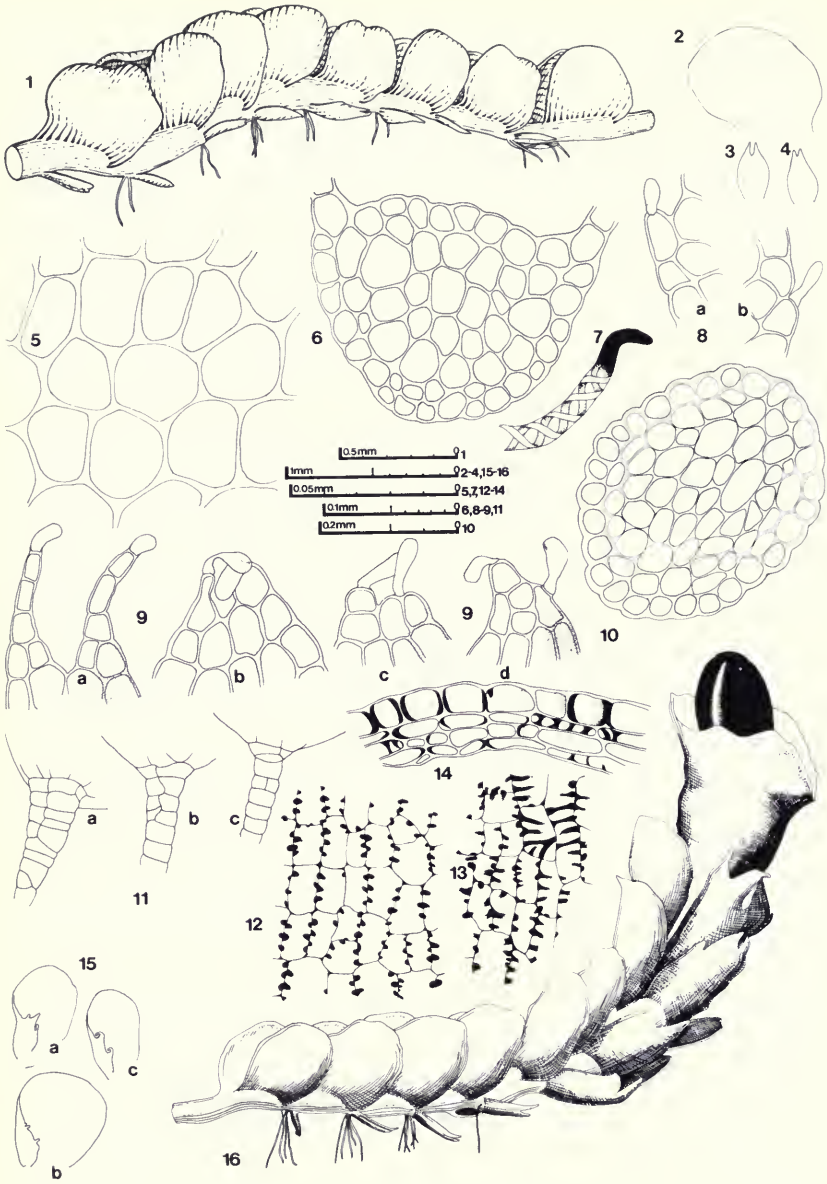
Chiloscyphus nigrescens Lindenb. & Hampe *in* Hampe, Linnaea 24:640. 1851, *syn. fide* Grolle (1960). Original material: Costa Rica, (crateris) Reventado, 3,050 m., *Oersted* (S!).

Notoscyphus variifolius Mitt. J. Linn. Soc., Bot. 16:188. 1877, *syn. fide* Stephani (1901). Original material: South Africa, Cape Prov., Cape of Good Hope, *Eaton* (NY!).

Clasmatocolea heterostipa Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15:441. *pl. 20.* 1885, *syn. cf.* Grolle (1959). Original material: Ecuador, "Andes Quintensis," M. Pichincho, 2,700-3,400 m., *Spruce* (M! — c. sporo., MANCH! — c. ♂).

Nardia lindmanii Steph. Bih. Kongl. Svenska Vetensk.-Akad. Handl. 23 (III, 2):25. 1897, *syn. fide* Grolle (1964). *Alicularia lindmanii* (Steph.) Steph. Bull. Herb. Bossier 1 (5):481. 1901 (= Spec. Hep. 2:43). *Notoscyphus lindmanii* (Steph.) Schiffn. Hedwigia 51:276. 1912. Original material: Brazil, R. Grande do Sul, Porto Alegre, *Lindman 42* (G! — c. sporo. + ♂, hb. Grolle!, M!).

Clasmatocolea chilensis Steph. Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26 (III, 6):33. 1900, *syn. cf.* Grolle (1956). Lectotype (*nov.*): Chile, Prov. Concepción, Concepción, 5 September 1896, *Dusén 166* (G! — c. sporo.).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Lophocolea turbiniflora Steph. Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26 (III, 6):45. 1900, *syn. fide* Grolle (1960). Lectotype (*nov.*): Chile, Prov. Valparaíso, Valparaíso, El Salto, *Dusén 139* (G!).

Lophocolea flavovirens Steph. Kongl. Svenska Vetenskapsakad. Handl. 46 (9):44. *f. 19 d-g.* 1911, *syn. cf.* Grolle (1956). *Clasmatocolea flavovirens* (Steph.) Herz. Acta Horti Gothob. 15:159. 1943. Lectotype (*cf.* Grolle 1956): Chile, Prov. Chiloé, I. Guafo, Cta. Samuel, 25 July 1908, *Halle 201* (UPS! — c. sporo.; isolectotypes: G!, JE!).

Lophocolea ligulata Steph. Kongl. Svenska Vetenskapsakad. Handl. 46 (9):47. *f. 17 e, f.* 1911, *syn. fide* Grolle (1960). Lectotype (*nov.*): Chile, Prov. Chiloé, I. Guafo, (Cta. Samuel), *Skottsberg* (G! — c. per.).

Lophocolea skottsbergii Steph. Kongl. Svenska Vetenskapsakad. Handl. 46(9):53. *f. 20 f.* 1911, *syn. fide* Grolle (1960). Lectotype (*nov.*): Chile, Prov. Chiloé, I. Chiloé, Ancud, *Skottsberg s. n.* (G! — c. per.).

Lophocolea boliviensis Steph. *in* Herzog, Biblioth. Bot. 21 (87):217. *f. 155.* 1916, *syn. fide* Grolle (1960) *non L. boliviensis* S. Arnell, Svensk Bot. Tidskr. 55:206. 1961. Lectotype (*nov.*): Bolivia, (Sillar, 1,800 m.), 1911, *Herzog 2778* (G 17765!).

Lophocolea longissima Steph. *in* Herzog, Biblioth. Bot. 21 (87):220. *f. 159 a.* 1916, *syn. nov.* Holotype: Bolivia, (R. Corani, ca. 1,800 m.), *Herzog 4671* (G! — c. ♂).

Alicularia grandistipula Herz. Biblioth. Bot. 21 (88):30. *f. 16.* 1921, *syn. fide* Grolle (1960) *non A. grandistipula* (Steph.) Horik. Hikobia 1:30. 1950. Holotype: Bolivia, Cord. de Quimsacruz, near Mine Viloco, 4,400 m., 1911, *Herzog 3183* (JE!).

Opposite:

FIG. 28. *Clasmatocolea vermicularis* (Lehm.) Grolle. **1,** Portion of axis, lateral view. **2,** Leaf. **3, 4,** Underleaves. **5,** Median leaf cells. **6,** Stem, cross section. **7,** Elater, apical portion. **8,** Underleaf margin with slime papilla. **9,** Underleaf apices showing slime papillae (some partially collapsed), roughed cuticle at lower right. **10,** Seta, cross section. **11a-c,** Antheridial stalks. **12,** Outer capsule wall cells. **13,** Inner capsule wall cells. **14,** Capsule wall, cross section. **15a-c,** Antheridial bracts. **16,** Perianth and sporophyte-bearing plant, lateral view. Figures 1-6, from type of *C. vermicularis*, *Ecklon*, South Africa, Cape of Good Hope; figures 7, 10, 14, 16, from *Halle 185*, Argentina, Prov. Chubut, Estancia Miguens; figure 8a, from *Esterhuysen E27342*, South Africa, near Joubertina; figures 8b, 9b, from *Arnell 1698*, South Africa, Gouna R.; figure 9a, d, from *Engel 3494*, Falkland Is., Cheeks' Cr.; figure 9c, from *Arnell 1695*, South Africa, Knysna; figures 11a-c, 15b, from *Schelpe 5140*, Natal, Karkloof; figures 1-13, from lectotype of *C. chilensis*, *Dusén 166*, Chile, Prov. Concepción, Concepción; figure 15a, from *Engel 3493*, Falkland Is., Cheeks' Cr.; figure 15c, from *Esterhuysen 25347*, South Africa, near Zondereinde.

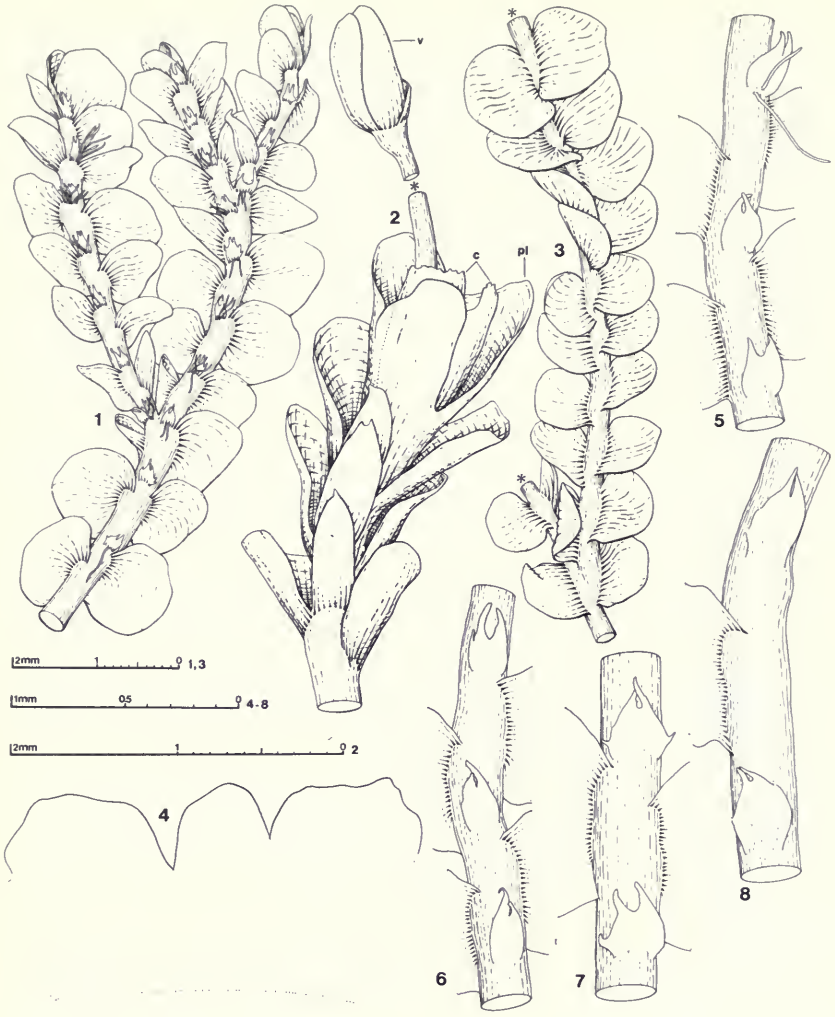


FIG. 29. *Clasmatocolea vermicularis* (Lehm.) Grolle. **1,** Axis, ventral view, with 2 *Frullania*-type branches. **2,** Apex of gynoecial shoot with sporophyte, ventral view (v = sporophyte valve; c = calyptra; pl = perianth lobe). **3,** Axis, dorsal view. **4,** Perianth mouth, ventral lobe in middle. **5-8,** Axes with distal portion of leaves removed, ventral view. Figures 1, 3, 7, from *Engel 11632*, Chile, Prov. Osorno, Salto del Indio; figures 2, 4, from *Engel 3939*, Chile, Prov. Osorno, L. Toro; figure 5, from *Engel 11083*, Chile Prov. Valdivia, Forestal Trafún; figure 6, from *Engel 12303*, Chile, Prov. Valdivia, Cord. Pellada; figure 8, from *Engel 11240*, Chile, Prov. Cautín, Salto Palguín.

Odontoschisma variabile Sim, Trans. Roy. Soc. South Africa 15:77. *unnumbered plate on p. 77.* 1926, *syn. cf.* Arnell (1958) *non O. variabile* (Lindenb. & Gott.) Trev. Mem. Ist. Lomb. Sci. Lett. III. 4:419. 1877. *Jungermannia variabilis* (Sim) S. Arnell, Bot. Not. 108:310. 1955, *nom. illeg.* Original material: South Africa, without specific locality, *sin. coll.* (*non vidi*).[7]

Lophocolea ovistipula Herz. Memoranda Soc. Fauna Fl. Fenn. 27:98. *f. 43 a-e.* 1952, *syn. cf.* Grolle (1959). Lectotype (*nov.*): South Africa, Cape Prov., Table Mt., ca. 600-900 m., 16 April 1922, *Rolfes 68* (JE!).

Lophocolea subulistipa Herz. Memoranda Soc. Fauna Fl. Fenn. 27:99. *f. 44 a-e.* 1952, *syn. fide* Grolle (1960). Holotype: South Africa, Natal, Sandymount, 1922, *Rolfes 136 p. p.* (JE!).

Lophocolea elata f. *aquatica* Herz. Feddes Repert. Spec. Nov. Regni Veg. 57:164. 1955, *syn. fide* Grolle (1960). Holotype: Colombia, Eastern Cord., La. de Cunta, edge of Páramo de Santurbán, 3,880 m., 1927, *Killip & Smith 17973* (JE!).

Lophocolea minima S. Arnell, Results Norweg. Sci. Exped. Tristan da Cunha 3 (42):18. *f. 14 a-d.* 1958, *syn. fide* Grolle (1960). Holotype: Inaccessible I., NE of Blendon Hall, 3-4 m., *Christophersen & Mejland 2431* (O!).

Plants rather soft, prostrate, but axes often sharply curved dorsally or ventrally, *usually pale green*, occasionally brown, commonly so when dry, very rarely rose tinted (several axes in a single collection—*Engel 3494*); axes to 2 cm. tall, 2.7 mm. wide.

Branches sparing, prostrate or arched, *intercalary branches mostly ventral, rarely lateral, terminal branches occasional*, of Frullania-*type*.

Stems fleshy, 6-9 cells high, cortex in 1-2 rows of slightly thick-walled cells the same size or slightly smaller than the medullary cells; endophytic hyphae occasionally present in both cortex and medulla. Rhizoids, when present, in fascicles from stem near underleaf base.

Leaves with insertion very slightly recurved at ventral end; leaves usually erect, occasionally spreading, distant to imbricate, weakly to moderately to distinctly *concave*, occasionally ± plane (especially in weak forms), *ovate to oblong or subquadrate or suborbicular* (those on branches and depauperate stems small, often obcordate-cuneate); apex broadly rounded to subtruncate to occasionally subretuse, very rarely bifid (toward bases of poorly developed axes); *margins and apices entire;* dorsal margin not or barely decurrent.

Leaf cells thin walled, trigones usually absent to small, occasionally medium; median leaf cells 18-35(-42) μ wide, 24-36(-48) μ long; cuticle smooth or roughened and appearing finely granular. Oil-bodies colorless, very finely granulose-papillose, ellipsoid to globose, consistently 2-3 per leaf cell, 7-13 × 6-8 μ.

[7] I have been unable to locate original material of *O. variabile* Sim. It is not in PRE or S; Arnell (1958) states he has seen the type, but does not indicate the herbarium in which it is housed.

Underleaves highly variable in size, *narrower than stem* (*normally slightly so*), transversely or obliquely inserted, *usually free*, occasionally weakly connate on 1 side, *weakly spreading* (occasionally distinctly so), remote, slightly convex to slightly concave (ventral view), *narrowly ovate to lanceolate to subulate; apices undivided and acute* (less often narrowly rounded), *or very often bidentate, or to 0.3(-0.5)-bifid;* segments directed toward stem apices or incurved, narrowly lanceolate-subulate or merely reduced to a slime papilla, the segments terminating in a slime papilla, *the sinus narrow; margins of the lamina entire*, or with 1 slime papilla, or with 1 small tooth terminating in a slime papilla.

Plants dioecious; androecia terminal or intercalary on leading axes or rather short branches, bracts with basal portion strongly saccate, the distal portion strongly concave or saccate in basal half, with distal portion moderately recurved; lobule margin with 2-several slime papillae that are often accompanied by 1 or 2 few-celled teeth, each terminating in a slime papilla; antheridia solitary, stalks biseriate throughout, or biseriate and with scattered uniseriate areas or uniseriate *and* with a few biseriate areas.

Gynoecia on leading axes; subfloral innovations occasionally present, originating from below gynoecium, from below perianth, or from inside perianth; vestigial stem perigynium present; bracts in 2-3 series, ± appressed to perianth, the bracts of innermost series usually with lateral margins free, occasionally with one complete margin fused with perianth, the bracts ovate to elliptic; apices ± truncate or retuse; margins entire or with a single tooth on ventral margin, rarely with both dorsal and ventral margins 1-dentate. Bracteoles of innermost series free from bracts, the lateral margins free, very rarely with 1 complete lateral margin fused with perianth; bracteoles ovate or lanceolate, very rarely broadly obovate; apices undivided and acute or broadly rounded, more often emarginate or bidentate or bifid to ca. 0.3; lamina margins entire or often with 1 or both margins with a single tooth or slime papilla, rarely laciniate. *Perianth large, subterete, or obscurely to distinctly trigonous, clavate to campanulate; perianth mouth wide and open*, the lobes occasionally free for ca. 0.3 perianth length, *the three lobes broadly rounded*, often undulate, often incurved, *entire*, rarely with the lateral or just the ventral lobe bidentate or bilobed; keels occasionally winged, secondary wings occasionally present. *Calyptra large*, often extending to perianth mouth.

Seta 5-10 cells in diameter, with 16-31 rows of outer cells surrounding an inner core of scattered cells equal to or slightly larger than outer row. Capsule oblong to globose, the valves 0.53-0.77 mm. long, 36-54 μ thick, of 3-4 layers, the outer row of cells 17-24 μ thick, equal to thickness of any 2 of interior strata; outer layer with red-brown, nodule-like thickenings that are frequently feebly tangentially dilated, semiannular bands absent; intermediate and inner layers of cells subequal in thickness, delicate, often collapsing; inner layer of cells 6-11 μ thick, with red-brown nodulose thickenings on radial walls similar to those of outer layer, the thickenings often tangentially dilated, semiannular bands often present.

Spores large, 15-20 μ, yellow-brown, exine with the light microscope appearing minutely punctate, but under the SEM with a network of wide, rather short, vermiform ridges covered with often crowded nanogranules, the intervening hollows between ridges sometimes with isolated nanogranules; spores averaging 1.9 × elater diameter. Elaters 6-12 μ wide, slightly tapered toward the ends, apical portions often with thick non-spiral walls, elater walls yellow-brown, 3-5 μ in diameter.

Variation.—Clasmatocolea vermicularis exhibits considerable variability, especially with regard to color, axis stature, the size, concavity, and

configuration of leaves and the configuration, apices (especially the sinus depth), and the disk marginal armature of underleaves. The leaf cells may have trigones absent to medium. See Grolle (1960, pl. 3, but with erroneous legend) for figures illustrating leaf and underleaf variation. As Grolle (*loc. cit.*) indicates, the variations listed above occur in all combinations and without regard to geography.

The gynoecia of type material of *Nardia lindmanii* present an interesting variant. The ventral margin of the bract nearest the perianth is completely fused with the perianth. In addition, one complete margin of the bracteole of the innermost series is likewise fused. The bracteole shape is also deviant, being broadly obovate with apices undivided and broadly rounded. See Schiffner (1912) for a discussion of this species, which he transfers to *Notoscyphus*.

Spruce (1885) and Stephani (1906) state the perianth mouth of *C. heterostipa* is three-four lobed, whereas Schiffner (1893) states the perianth mouth is two-four lobed in the genus. *Clasmatocolea vermicularis* (= *C. heterostipa*), however, always has three lobes (fig. 29-2, 4). These lobes are nearly always broadly rounded and entire and only rarely is the lateral or just the ventral lobe bidentate (as in several New Zealand collections) or more deeply divided (as in pl. 1, fig. 1, in Grolle, 1956).

Differentiation.—Clasmatocolea vermicularis may be separated from all other *Clasmatocolea* taxa by the following ensemble of features: (a) the ovate-oblong or suborbicular or subquadrate leaves that are *at least slightly adaxially concave;* (b) the mostly narrowly ovate to lanceolate to subulate underleaves that are narrower than the stem width; (c) the underleaf apices that are usually bidentate or divided to at most 0.3(-0.5), and with lamina margins entire or with 1 small tooth; and (d) the clavate to campanulate, inflated perianths with mouths wide and open and with lobes broadly rounded and nearly always entire.

Some phenotypes of *C. vermicularis* that do not possess distinctly adaxially concave leaves may offer some confusion with *Lophocolea sabuletorum*. *Clasmatocolea vermicularis* has leaves that exhibit at least a slight concavity and have leaf apices broadly rounded or truncate, at most subretuse, and never emarginate or dentate. *Lophocolea sabuletorum* has at least some leaves slightly convex, and with leaf apices variable, *i.e.*, broadly rounded to truncate or often retuse to emarginate to 1- or bidentate. *Clasmatocolea vermicularis* and *L. sabuletorum* not infrequently have androecia, the antheridial stalk of which will immediately distinguish the taxa, with *C. vermicularis* having at least locally biseriate stalks, and *L. sabuletorum*, uniseriate stalks.

Jungermannia subintegra was described from the Falkland Islands and is

a synonym of *C. vermicularis*. This treatment is based upon examination of a syntype of the former species and also upon the work of Grolle (1960). Mizutani & Hattori (1959), however, treat the species as a synonym of *Lophocolea novae-zelandiae*. There should be little confusion concerning the disposition of *J. subintegra*, because the adaxially concave leaves immediately place the plant within the genus *Clasmatocolea*.

If sterile South African plants are at hand, *C. vermicularis* may be confused with the superficially similar *Notoscyphus belangerianus* (Lehm.) Mitt. The two taxa may be easily separated by examining leaf preparations—*N. belangerianus* has a striate-papillose leaf cuticle and large to knotlike trigones.

Notes.—1. In a packet glued to the sheet with syntype plants of *Jungermannia subintegra* are several plants of *Lophocolea sabuletorum* (leaf apices frequently emarginate, antheridial stalk cells unistratose). These plants should not be confused with those of the type.

2. Grolle (1960) has referred to *Lophocolea ligulata* as a "nomen mixtum," because the original specimen contains material of both *C. vermicularis* (*p.p. maj.*) and *L. sabuletorum* (*p. p. min.*), and the original diagnosis contains portions from both species. The description of the perianth was based upon material of *C. vermicularis*, and that of the sterile structures on material of *L. sabuletorum*. Grolle (*loc. cit.*) has typified the specimen as one of *C. vermicularis* (because most of the material is of this taxon), but he was in error, however, in stating Stephani originally described *L. ligulata* as monoecious. Grolle has extracted several portions of Stephani's description in *Species Hepaticarum* (vol. 6, p. 280, 1922); Stephani's original description (1911) clearly states his new species is dioecious.

I have seen two Halle-collected specimens (c. per. + sporo.) of *L. ligulata* from the Uppsala Herbarium and one collected by Skottsberg (c. per.) from the Geneva Herbarium. Stephani (1922) effectively eliminates the Halle collections from further consideration as lectotype candidates because he lists only Skottsberg as the collector.

3. Of the eight syntype localities listed by Stephani (1911) for *Lophocolea skottsbergii*, only one (Isla Chiloé, Ancud) is given for the species in Stephani (1922). Stephani, in the latter publication, has effectively lectotypified the species. Among the plants of the lectotype (G), there are some with suborbicular leaves and others with oblong leaves. Stephani notes only suborbicular leaves in his original description. The syntype specimens from Río Olivia, near Ushuaia are of *C. humilis*.

4. Grolle (1960) lists *Odontoschisma africanum* (Pears.) Sim as a "pseudosynonym" of *C. vermicularis*. As discussed in Grolle (*loc. cit.*), the basionym of *O. africanum* is *Cephalozia denudata* var. *africana* Pears. and is

actually a specimen of *Odontoschisma*. However, the description and plate of *O. africanum* in Sim (1926) plus his herbarium specimens are actually *C. vermicularis*. Arnell (1955b) utilized the information in Sim (*loc. cit.*) rather than that of the original description and type and mistakenly made the combination *Notoscyphus africanus* (Pears.) S. Arnell (*nom. illeg.*). Specimens of *N. africanus* are actually *C. vermicularis*. Arnell (1963) later recognized *Odontoschisma africanum*.

5. Herzog (1952, p. 98) states for the locality of *Lophocolea ovistipula:* "Kapland: Tafelberg, an feuchten Steinen und Felsen, leg. L. Rolfes, IV. 1922". Among the specimens of *L. ovistipula* labeled "Herbarium Theodor Herzog Jena" (JE) are three syntypes, all of which bear the note "Herz. n. sp." Of the three, two (identical) are androecial specimens collected on Devils-Peak, but bear no ecological data. The third, however, is labeled "Tafelberg, feuchte Steine an Bachen" and is sterile. The third collection has been selected as the lectotype; it matches closely with the locality, plate, and description data, including the lack of sex organs.

6. The protologue and original material of *Lophocolea boliviensis* Steph. (Stephani, 1916) contains elements of both *C. vermicularis* and *Jungermannia* sp. Stephani's description and figure of the perianth are referable to plants of *Jungermannia*, whereas the description and figure of the underleaves, plus the description of at least some of the other sterile features, belong to *Clasmatocolea*. There were several problems involved with typification, as illustrated in the following discussion of the specimens studied.

Specimen 1: G 17765, leg. *Herzog 2778*, which by collection number is referable to the specimen from Sillar, Bolivia. The plants are of *C. vermicularis* and look much like Stephani's figure (a). However, the underleaves are not connate on both sides (as in the diagnosis and figure) but only on one side, with the second underleaf margin in close proximity to the leaf base. I did not observe leaves with the broad tooth as in the Stephani figure. There was a single well-developed perianth present—it was of *C. vermicularis*. No plants of *Jungermannia* were observed, but a few reddish plants were seen.

Specimen 2: G 17766, leg. *Herzog 2778*, and thus also from Sillar. This appeared to be a duplicate of G 17765, but in this case there were no perianths, but rather some androecial individuals. Like the above, no *Jungermannia* was found.

Specimen 3: JE collection of *Herzog 3869* and labeled "Bei Altamachi," and thus is the second of two localities mentioned in the protologue. The plants of *C. vermicularis* have underleaves free and not with *both* margins

FIG. 30. *Clasmatocolea vermicularis* (Lehm.) Grolle.

in close proximity to the leaf bases. Intermixed were sterile plants of *Jungermannia* sp., leaving me with the mystery of the origin of the perianth data in the protologue.

The specimen of G 17766, being closest to the concepts embodied in the protologue, was selected as lectotype.

7. Nearly all collections of this species in New Zealand were thought to be *C. strongylophylla*, with a few identified as *C. paucistipula.*

8. See Grolle (1960) for additional remarks on *C. vermicularis;* see also his pl. 1. Refer also to Grolle (1956) for comments (sub *C. heterostipa*); see also his pl. 1.

Ecology.—Frequently on shaded, damp earth or rocks of stream or riverbed or banks. Here the plants are subject to inundation during wet seasons or periods of flooding, but then become exposed or grow just above water level during drier periods. Also, in either forests or exposed sites on dripping rock walls, steep, often irrigated slopes of gulleys or gorges, or clayey banks. Occasionally over calcareous sandstone (New Zealand). Not uncommon on roadside banks. For notes on ecology in Colombia see Gradstein et al. (1977, p. 392-393).

Phytogeography.—Pan-temperate; New Zealand, South I. (455-1,830 m.), North I. (300-1,500 m.), Great Barrier I. (275 m.); Tasmania (1,250 m.); Kerguelen; Crozet Is.; Marion I. (25-100 m.); Mascarene Is., Réunion (1,550-1,570 m.); Madagascar (900-2,200 m.); South Africa, Cape Prov. (215-900 m.), Natal (1,200-2,440 m.), Transvaal (795 m.); Rhodesia (1,435 m.); Zaïre (2,080 m.); Tanzania (1,500-1,725 m.); Burundi (1,340-2,050 m.); Tristan da Cunha Group, Inaccessible I. (3-4 m.), Tristan da Cunha (sea level-700 m.); South Georgia; Falkland Is. (sea level-75 m.); Chile, rare in Tierra del Fuego, sporadic in Patagonian Channels, Valdivian region (140-1,600 m.), Prov. Valparaíso (20-30 m.), Prov. Santiago (1,200 m.); Argentina, Prov. Chubut, Prov. Río Negro (1,800 m.), Prov. Neuquén (820 m.); Juan Fernández Is. (150-550 m.); Brazil; Bolivia (1,800-4,470 m.); Peru (2,000-3,600 m.); Ecuador (2,700-3,400 m.); Colombia (2,500-4,520 m.); Venezuela (3,500 m.); Costa Rica (1,500-3,050 m.) (see fig. 30).

Specimens seen.—**NEW ZEALAND. SOUTH ISLAND.** OTAGO: Bank of Matau Branch of Clutha R., near Kaitangata, *Allison s.n.* (hb. Grolle); ibid., *Allison H6413*, *H6818* as *C. strongylophylla* (CHR); Dunedin, Signal Hill, *Allison H1412* as *C. strongylophylla* (CHR); Old Man Range, below The Old Man, ca. 1,220 m., *Schuster 67524* as *C. strongylophylla* (hb. Schuster); Pigroot, 3 mi. from Kyeburn, 455 m., *Child 1683* as *C.* ? *strongylophylla* (hb. Child, F); Danseys Pass, near Naseby, ca.

940 m., *Irwin 16 p.p.* as *C. strongylophylla* (CHR); Naseby, ca. 600 m., *Allison H5443* as *C. strongylophylla* (CHR); St. Bathans, *McConnochie 421, 432* as *C. strongylophylla* (hb. Monash Univ.). WESTLAND: Fiordland, Olivine Mts., upper Dart Valley, ca. 1,830 m., *Campbell s.n.* as *C. zotovii* (CHR); Regina Valley, 1,220 m., *Teague s.n.* as *Lophocolea austrigena* (CHR). MARLBOROUGH: Pelorus R., *Martin H601* as *C. paucistipula* (CHR). **NORTH ISLAND:** *Sin. loc., Berggren 3701* as *L. paucistipula* (LD). WELLINGTON: Wairarapa, near Tinui, *Hewitt s.n.* (hb. Grolle); Cross Cr., Haast Road, ca. 460 m., *Child 1896* as *C. strongylophylla* (hb. Child, F); Kaimanawa Range, 1,500 m., *Druce s.n.* (hb. *Grolle*). HAWKE'S BAY: Kiwi Valley, Wairoa, *Hodgson 4153* (hb. Grolle). GISBORNE: Rosie B., L. Waikaremoana, *Hodgson 8387* (CHR, hb. Grolle — c. ♂); Te Tara-a-Tu Pillar, Mt. Maungapohatu, Urewera, 1,065 m., *Sainsbury s.n.* as *C. strongylophylla* (CHR). SOUTH AUCKLAND: Taupo, *Berggren 3704* as *L. paucistipula* (LD); Kaingaroa Plains, near Rotorua, *Allison H3718* as *C. strongylophylla* (CHR); ibid., *Allison 328* — c. sporo. (hb. Grolle); plateau E. of Waiotapu Valley, 550 m., *Allison H3566* as *C. strongylophylla* (CHR); ibid., 600 m., *Allison 326* (hb. Grolle); near Atiamuri, S. of Rotorua, *Allison H387* — c. sporo., *H470* — c. per. as *C. paucistipula* (CHR); ibid., ca. 305 m., *Allison H388, H3369* as *C. strongylophylla* (CHR); ibid., 305 m., *Allison s.n.* as *C. strongylophylla* (hb. Child, F); ibid., *Allison H3369* as *C. rotata* (hb. Grolle); Cormandel Pen., *Matthews 37* as *C. paucistipula* (CHR). **GREAT BARRIER ISLAND:** Hauraki G., Kiwiriki B., 275 m., *Lloyd 219* as *L. austrigena* (CHR). **TASMANIA:** Cradle Mt. Region, Plateau Cr. area, between Cradle Plateau and Marions Lookout, NNW of Cradle Mt., 1,250 m., *Engel 13974* (F); Cradle Mt. Region, Marigold Cr., W. of and draining into Crater L., vicinity of Crater P. Lookout, 1,250 m., *Engel 14108* (F). **KERGUELEN:** *Moseley s.n.* (hb. Grolle). **CROZET IS.:** I. Possession, Port Alfred, *Hebrard 10* (JE); I. de l'Est, Vallée du Naufrage, *Hebrard 40* (JE); I. de l'Est, Cap Nord, *Hebrard 67/a* (JE). **MARION I.:** *Rand 3782* (hb. Grolle); SW of Met. Station, 25 m., *Huntley 119c* (hb. Grolle); Macaroni B., 25 m., *Huntley 916* (hb. Grolle, PRE); N. of Juniors Kop, 100 m., *Bakker 18b* (hb. Grolle). **MASCARENE IS. RÉUNION:** Plaine d'Affouches, *Hebrard 24/a* (JE); Plaine des Cafres, 1,550-70 m., *Gimalac 74. R. 8341, 74R. 8382* (JE). **MADAGASCAR:** Forêt de Ranomafana, 60 km. N. of Fianarantsoa, ca. 900 m., *Onraedt 71.M. 5061* (hb. Grolle); Soavimbahoaka, above Tananarive, *Onraedt 71. M. 5197* (hb. Grolle); Omkaratra, ca. 2,200 m., *Cremers 2381* — c. per. (JE). **SOUTH AFRICA.** CAPE PROV.: "Kapland," *sin. coll.* as *Chiloscyphus vallisgratiae* Gott. (JE); ibid., *sin. coll.* as *Jungermannia congesta* (JE); Peninsula, Chapmans P., *Ar-*

nell 1127 as *L. ovistipula* (BOL); Peninsula, Constantianek, *Arnell 169*, *171*, *181* (BOL); ibid., *Arnell 170*, *318* (UPS); Peninsula, Rhodes Road, near Constantianek, 215 m., *Garside 6685*, *6693* (UPS); Table Mt., Constantianek, *Arnell 181* (UPS); Table Mt., Silverstream Ravine, 915 m., *Esterhuysen 25113* as *L. ovistipula* (UPS); Peninsula, Oranjekloof, *Arnell 2160*, *2165*, *2185*, *2210* (BOL); ibid., *Arnell 2200* (PRE); ibid., *Arnell 2183* (UPS); Tafelberg, 600-900 m., *Rolfes s.n.* as *Lophocolea subrotunda* (JE); ibid., *Rolfes s.n.* as *L. ovistipula* fo. *aquatica* (JE); Devils P., *Arnell 2215* as *L. ovistipula* (BOL); ibid., 300-400 m., *Rolfes 85* as syntype of *L. ovistipula* — c. ♂ (JE); Groot Drakenstein, near Stellenbosch, *Cholnoky s.n.* as *L. subulistipa* (UPS); near Kirstenbosch, *Arnell 171* as *L. ovistipula* (BOL); Caledonrivier, Riviersonderend Reeks, near Greyton, 610 m., *Esterhuysen 21103* as *L. subulistipa* (UPS); Riviersonderend Reeks, near Zondereinde, *Esterhuysen 25347* — c. ♂ (UPS); Du Toitskloof, *Esterhuysen 19887*, *25413* (BOL); Kromrivierkloof off Du Toitskloof, *Esterhuysen 25412* as *L. subulistipa* (UPS); ibid., *Esterhuysen 25413* as *L. ovistipula* (UPS); foot of Waaihoek P., 305-610 m., *Esterhuysen 24151* as *L. ovistipula* (BOL, UPS); Gouna Forest Station, *Arnell 1695* (UPS); ibid., Gouna R., *Arnell 1698*, *1710* (UPS); N. foot of Tsitsikama Mts., near Joubertina, *Esterhuysen 27342* as *L. subulistipa* (UPS); Baviaanskloof, *Esterhuysen 24996* as *L. ovistipula* (BOL). NATAL: near Escourt, *West s.n.* (UPS); Braco, Karkloof, 1,220 m., *Schelpe 5140* (BOL, UPS — c. ♂); Cathedral P. Forest Station, Catchment no. 1 Research Area, *Magill 5650* (F); Mont Aux Sources, Koedoepas, 2,440 m., *Sim 1613* as *L. subulistipa* (UPS); Zululand, Ngome-Bosreserwe, 1,200 m., *Oliver 7096* (F). TRANSVAAL: Farm Oshoek, E. of Wakkerstroom, *Tölken s.n.* (F); Forst Ceylon, near Sabie, *Cholnoky s.n.* (UPS); Bonnet Junction and Mac-Mac Falls, near Sabie, *Cholnoky s.n.* as *L. ovistipula* — c. ♂ (UPS); 5 mi. SW from Duivelskloof, 795 m., *Schelpe 6031* as *L. ovistipula* (BOL, UPS). **RHODESIA:** Umtali, near Odzani R. Bridge, 1,435 m., *Schelpe 5650* as *L. ovistipula* (BOL, UPS). **ZAÏRE:** Near Uvira, S. of Kwamwalimu, 2,080 m., *Symoens 2153* (hb. Vanden Berghen). **TANZANIA:** Kilimanjaro, near Kibo Hotel, 1,500 m., *Esterhuysen 27263* as *L. ovistipula* (UPS); Southern Highlands, N. foot of Mt. Kyejo, E. of Tukuyo town, 1,725 m., *Pócs 6769/B* (hb. Váňa). **BURUNDI:** S. of Rutana, near Mutambala, 1,340 m., *Symoens 2762a* (hb. Vanden Berghen); near Muramvya, 2,050 m., *Symoens 2384* (hb. Grolle — c. per., hb. Vanden Berghen). **TRISTAN DA CUNHA:** 620-700 m., *Christophersen & Mejland 42*, *51* as *L. skottsbergii* (O); 30-60 m., *Christophersen & Mejland 198*, *310* as *L. strongylophylla* (S); 650 m., *Christophersen & Mejland 839* as *L. strongylophylla* (S). **SOUTH GEORGIA:** Cumberland B., *Skottsberg 231*

as syntype of *L. skottsbergii* — c. ♂ (L). **FALKLAND IS.** (selected): *Hooker s.n.* as *Lophocolea grisea* — c. ♂ (NY); *Skottsberg s.n.* as syntype of *L. skottsbergii* — c. per. (G). **EAST FALKLANDS:** Port Louis, *Halle & Skottsberg 236* as *Lophocolea vasculosa* (NY); ibid., *Skottsberg s.n.* as *L. austrigena* — c. per. (S); Port William Region, N. shore of Cape Pembroke Peninsula, E. of Yorke Pt., *Engel 2446* (MSC). **WEST FALKLANDS:** Fox Bay Region, near mouth of Cheek's Cr., ca. 12 m., *Engel 3493* — c. ♂, *3494* — c. ♂, *3495* (MSC). **ARGENTINA.** TERR. TIERRA DEL FUEGO: I. de los Estados, Pto. San Juan del Salvamiento, *Spegazzini 83* as *Lophocolea grisea* v. *lava* ? (NY); I. de los Estados, Pto. Basil Hall, *Spegazzini 86* as *L. grisea* v. *lava* ? (NY). **CHILE.** PROV. MAGALLANES: Brunswick Pen. (cf. Engel, 1978); S. Skyring, Cabo Leon, *Hatcher* coll. (cf. Engel, 1973); S. Skyring, B. Pinto, *Halle & Skottsberg 231* as syntype of *L. skottsbergii* (BM). PROV. AISÉN: Cta. Conner, *Halle 201* as syntype of *L. flavovirens* (UPS); I. Magdalena, *Schwabe 20/1* as *Lophocolea minuta* (JE); C. Tesoro, 1,000 m., *Schwabe 39 c p.p.*, *39/6*$_2$ as *Lophocolea tesorensis* Herz., **nom. hb.** (JE). PROV. CHILOÉ: I. Guafo, C. Samuel, *Halle s.n.* — c. per. (hb. Grolle); ibid., *Halle 216* as syntype of *L. ligulata* — c. per. + sporo. (UPS); I. Chiloé, Quemchi, *Skottsberg 201* as syntype of *L. flavovirens* (UPS). PROV. LLANQUIHUE: Calbuco, *Schwabe s.n.* (hb. Grolle); ibid., *Schwabe 35* (JE); ibid., *Schwabe 54* — c. sporo., *171* as *C. heterostipa* (JE); ibid., *Schwabe 125* as *L. skottsbergii* (JE); Puerto Varas, *Dusén s.n.* as syntype of *C. chilensis* (BM, LD — c. per.); ibid., *Dusén 473* as syntype of *C. chilensis* (UPS). PROV. OSORNO: L. Rupanco, *Schwabe 51* as *C. heterostipa* (JE); L. Toro, on road to Refugio Antillanca, 860 m., *Engel 3977*, *3989* — c. sporo. (MSC); valley of R. Nauto near road to Refugio Antillanca, between La. El Encanto and L. Toro, 730 m., *Engel 4080*, *4105A* — c. sporo. (MSC); Termas de Puyehue, *Schwabe 111* (hb. Grolle). PROV. OSORNO near Prov. Valdivia boundary: Anticura, Salto del Indio, 19 km. by road E. of Termas de Puyehue along international highway, 300 m., *Engel 11632*, *11638*, *11644* — c. sporo. (F). PROV. VALDIVIA: W. slope of Cord. Pelada, W. of El Mirador on road between La Union and Pta. Hueicolla, 580 m., *Engel 12303* — c. per. (F); Corral, *Krause s.n.* as *Leioscyphus chamissonis* (S); ibid., Amargos, *Hosseus 835* — c. ♂, *846* as *C. heterostipa* (JE); Panguipulli, 140 m., *Hollermayer 662*[a] as *Leioscyphus chamissonis* (JE); Forestal Trafún, *Engel 11083* (F); L. Pellaifa, *Schwabe 9 p.p.* as *L. subintegra* fo. *humilis* (JE); SW of La. Los Patos, SW slope of V. Quetrupillán, 1,450-1,600 m., *Engel 11133* (F). PROV. CAUTÍN: Termas de Palguín, along R. Palguín, 730 m., *Engel 11316* (F); Salto Palguín, R. Palguín, road to Termas de Palguín, 580 m., *Engel 11240* (F); Pucón, *Hosseus 170* as *C.*

heterostipa — c. ♂ (JE, M); Parque Nac. Conguillo, El Salto, 1,110 m., *Mahu s.n.* — c. ♂ (hb. Mahu). PROV. MALLECO: Mininco, *Schwabe 157/e* (hb. Grolle); Parque Nac. Nahuelbuta, casa de Pincheira, 1,250 m., *Mahu 6037* (JE, hb. Mahu); ibid., *Mahu 6093* (hb. Grolle, hb. Mahu). PROV. MALLECO/PROV. ARAUCO: Cord. Nahuelbuta, Aguas Calientes, Parque Nac. Nahuelbuta, ca. 48 km. W. of Angol, 1,240 m., *Engel 12614* (F). PROV. CONCEPCIÓN: Concepción, *Dusén s.n.* as syntype of *C. chilensis* (BM); ibid., *Dusén 157* as syntype of *C. chilensis* (G — c. per., S); ibid., *Dusén 161* as syntype of *C. chilensis* (BM — c. per., FH — c. ♂, G — c. per., O); ibid., *Dusén 346/2* as syntype of *C. chilensis* (M); Lota, *Skottsberg 159* as *C. flavovirens* (JE). PROV. VALPARAÍSO: Valparaíso, (El Salto), *Dusén s.n.* as syntype of *L. turbiniflora* (BM — c. ♂, LD); ibid., *Dusén 139* as syntype of *L. turbiniflora* (BM — c. ♂, FH, JE, O, S — c. ♂, UPS); El Quisco, Q. Guallelemu, 30 m., *Mahu 10327/a* (JE); ibid., 20 m., *Mahu 11374* (F), ibid., 20-30 m., *Mahu 11020, 11391* (hb. Mahu). PROV. SANTIAGO: Caleu, 1,200 m., *Mahu 8611* (hb. Grolle, hb. Mahu). **ARGENTINA.** PROV. CHUBUT: Colonia Diez-y seis de Octubre, *Halle 204* as *Lophocolea georgiensis* (UPS); ibid., *Halle 185* as *L. austrigena* — c. sporo. (S). PROV. RÍO NEGRO: L. Nahuel Huapí, C. de Los Hormigas, R. Ñirihuau, ca. 1,800 m., *Hosseus 626a* as *Lophocolea patulistipa* (JE). PROV. NEUQUÉN: L. Nahuel Huapí, I. Victoria, 820 m., *Sleumer 1722* as *L. diversistipa* (UPS). **JUAN FERNÁNDEZ IS.:** 150-200 m., *Kunkel 334/5a* (B); Mas a Tierra, head of Pangal Valley, *Hatcher & Engel 18* (JE); Mas a Tierra, base of Piramide, *Hatcher & Engel 534* (JE); Mas a Tierra, near Port. de Villagra, 550 m., *Hatcher & Engel 704* (JE). **BOLIVIA.** DEPTO. COCHABAMBA. PROV. QUILLACOLLO: Cord. del Tunari, above and SW of La. Marquina, 4,470 m., *Lewis 2510, 2517* (F). PROV. CHAPARÉ: R. Corani, ca. 1,800 m., *Herzog 4719* as *Chiloscyphus parvistipulus* — c. sporo. + ♂ (M). PROV. AYOPAYA: Altamachi, ca. 3,500 m., *Herzog 3869* as syntype of *L. boliviensis* (JE). **PERU.** PROV. OTUZCO: Casmiche, *Hegewald 6005* (hb. Hegewald); ibid., *Hegewald 6503* (hb. Hegewald, JE); C. las Gordas, between Quiruvilca and Agallpampa, 3,600 m., *Hegewald 5970* (hb. Hegewald, F); ibid., between Los Alisos and Quiruvilca, 3,600 m., *Hegewald 5975* (hb. Hegewald). PROV. CONTUMAZÁ: "Tambo de Lima," between Contumazá and Cascas, 2,000 m., *Hegewald 7379* (F, JE — c. per.); at Tunnel between Contumazá and Cascas, C. Ludén, 2,400 m., *Hegewald 7356* (F, JE). PROV. CAJAMARCA: Puente Bajo between Encañada and Celedín, 3,550 m., *Hegewald 6596* — c. per. (hb. Hegewald, JE). PROV. CHACHAPOYAS: Calla Calla, between Balsas and Leimebama, ca. 3,100 m., *Hegewald 6938* (hb. Hegewald, JE). **ECUADOR:** R. Cusatagua, near Quito, *Spruce*

s.n. as *Leioscyphus chamissonis* (MANCH). **COLOMBIA.** BOYACÁ: NW of Belén, Q. Minas, 3,800 m., *Cleef 2088a* (U, F). CUNDINAMARCA: Salto de Tequendama, ca. 2,500 m., *Schaeck 72 Am. 33* (hb. Grolle). **VENEZUELA:** Sa. de St. Domingo, 3,500 m., *Oberwinkler & Poelt HV69-10, HV69-25* (JE). **COSTA RICA.** PROV. CARTAGO: Ca. 10 km. SSE of Tapantí along road on E. slope above R. Grande de Orosi, 1,500-1,550 m., *Engel 8343, 8397* (F). PROV. SAN JOSE: La Palma area, above R. La Hondura valley ca. 9 km. NE of San Jerónimo, ca. 1,575 m., *Engel 8815, 8819* (F).

Clasmatocolea gayana (Mont.) Grolle. Figures 31-33, Plates 13-14.

Jungermannia gayana Mont. Ann. Sci. Nat. Bot. III. 4:349. 1845. *Chiloscyphus gayanus* (Mont.) G. L. & N. Syn. Hep. 710. 1847. *Lophocolea gayana* (Mont.) Mitt. *in* Seemann, Fl. Vit. 404. 1873. *Clasmatocolea gayana* (Mont.) Grolle, Rev. Bryol. Lichénol. 29:72. 1960. Original material: Chile, Prov. Valdivia, Valdivia, *Gay 44* (FH! — c. sporo., S!).

Lophocolea vinciguerreana Mass. Nuovo Giorn. Bot. Ital. I. 17:229. *pl. 18, f. 1-9*. 1885, *syn. fide* Bescherelle & Massalongo (1889). Lectotype (*fide* Engel, 1978): Chile, Prov. Magallanes, I. Basket, Cabo Desolación, June 1882, *Spegazzini 317* (VER!).

Conoscyphus flaccidus Pears. Bull. Misc. Inform. 1922:252. *1 pl.* 1922, *syn. nov.* Holotype: Chile, Prov. Magallanes, Punta Arenas, March 1868, *Cunningham 194* (BM!).

Plants *fleshy and soft*, prostrate, mixed with other bryophytes or in dense pure mats, *grey-green, highly nitid when dry; axes to 1.8 mm. wide, with apices and intercalary portions of axes very commonly enlarged, the axes often with a somewhat flattened appearance in ventral view.*

Branches frequent, *of lateral-intercalary type* (commonly from ventral end of merophyte) *and* Frullania-*type* (collections varying in predominance of each type), *ventral-intercalary vegetative branches not seen.*

Stems 6-9 cells high, *cortex undifferentiated* or more rarely in a single row of slightly larger cells, cortex and medulla with usually distinctly thick-walled cells, rarely with them only slightly thickened; endophytic hyphae absent. *Rhizoids in fascicles from a raised, flat, disciform rhizoid initial field confluent with median portion of underleaf base.*

Leaves with insertion moderately recurved at ventral end; *leaves strongly erect and axis then appearing narrowly channeled* in dorsal view, occasionally locally connivent, rarely connivent throughout axis, occasionally moderately spreading, *densely imbricate*, conchiform concave, *wide-ovate* to ± *oblate;* apex rather narrowly to very broadly rounded to ± truncate, undivided, *in moist condition the apical portion of leaves incurved, in dried condition the apical portion of at least some leaves of main axis strongly incurved, the apices with a few teeth or* (commonly) *entire;* dorsal margin ± straight, often sinuate, often in part reflexed, not or slightly decurrent, *with few to several often sharp teeth and/or blunt projections*, occasionally entire; ventral margin entire, very broadly

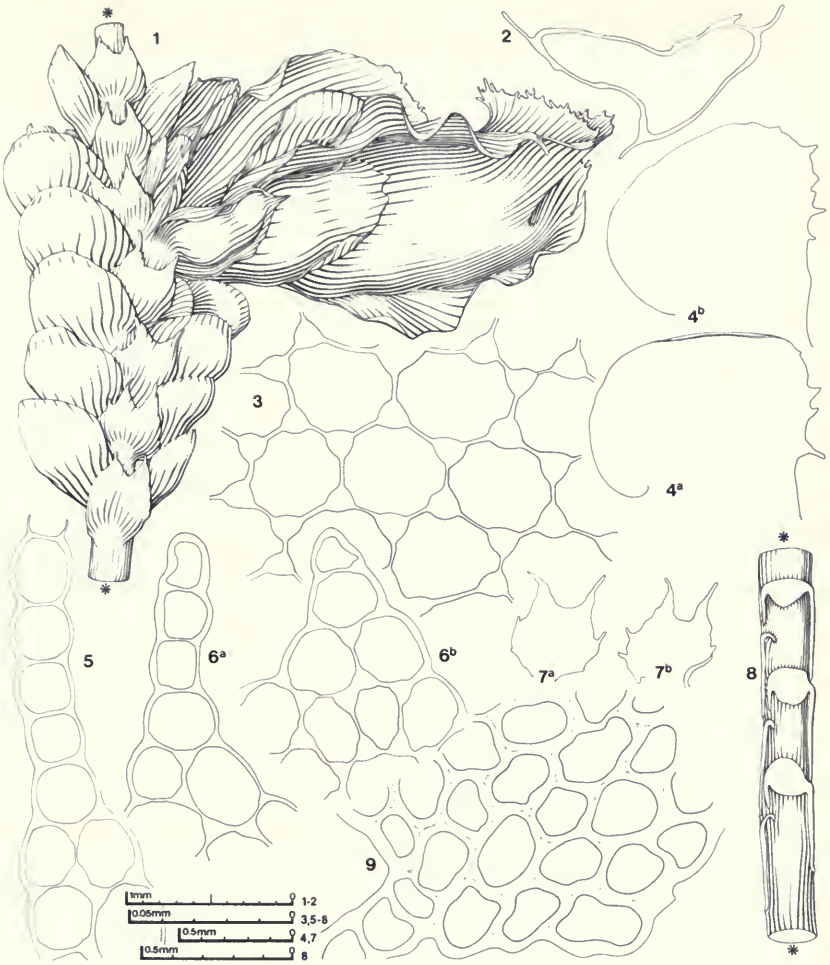


FIG. 31. *Clasmatocolea gayana* (Mont.) Grolle. **1,** Main axis with perianth, ventral view. **2,** Perianth with 3 keelar wings and a short secondary wing, cross section through median portion. **3,** Median leaf cells. **4,** Leaves. **5,** Underleaf segment, terminal portion with collapsed slime papilla. **6,** Teeth of dorsal margin of leaf. **7,** Underleaves. **8,** Main axis showing leaf and underleaf insertion, ventral view; note raised rhizoid initial fields. **9,** Stem, cross section. Figures 1, 3, 4a, 5-7a, from type of *C. gayana*, "Chile, hb. Montagne" (FH); figure 2, from *Engel 4554*, Chile, Prov. Magallanes, Pto. Edén; figures 4b, 7b, from *Engel 4225*, Chile, Prov. Chiloé, Pto. Ballena; figure 8, from *Engel 4473*, Chile, Prov. Magallanes, I. Williams; figure 9, from type of *C. gayana*, Chile, Valdivia, *Gay 44* (S).

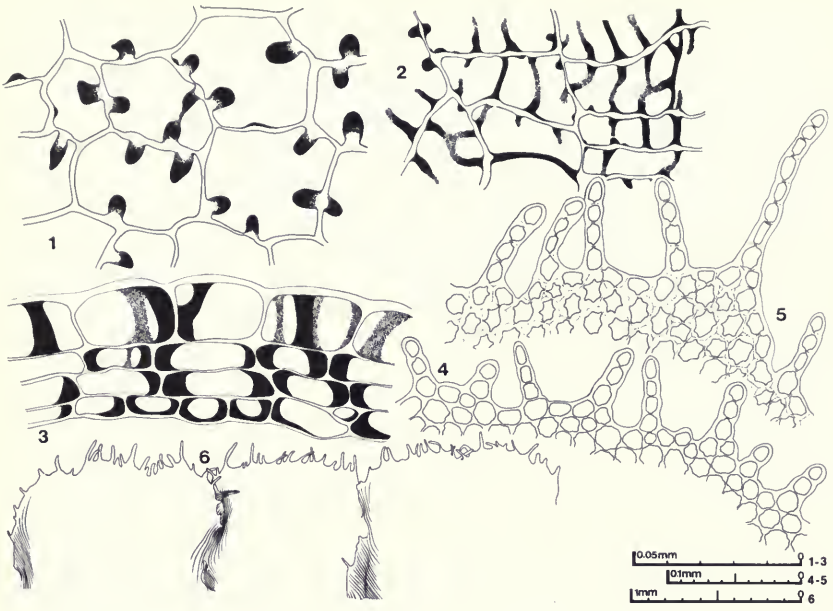


FIG. 32. *Clasmatocolea gayana* (Mont.) Grolle. **1,** Outer capsule wall cells, note semiannular band. **2,** Inner capsule wall cells. **3,** Capsule wall, cross section. **4,** Median apical portion of innermost bract. **5,** Perianth mouth. **6,** Perianth mouth, ventral lobe in middle. Figures 1-3, from *Imshaug 42959*, Chile, Prov. Osorno, near L. Toro; figure 4, from *Engel 4229*, Chile, Prov. Chiloé, Pto. Ballena; figures 5, 6, from *Engel 4554*, Chile, Prov. Magallanes, Pto. Edén.

rounded, the basal portion often extending across stem and closely approaching but not in contact with ventral margin of opposite leaf, the *ventral margin entire.*

Leaf cells thin-walled, *trigones bulging to nodular*, rarely confluent; median leaf cells 18-34 μ wide; 20-38(-42) μ long; cuticle smooth or roughened and appearing finely granular, sometimes a few cells with smooth cuticle scattered among cells with roughened cuticle.

Underleaves *1.5-2.2(-2.8)* $\times$ *stem width*, connate on 1 side, transversely or obliquely inserted, slightly spreading, *imbricate*, slightly to moderately convex (ventral view), ovate to subrectangular, *0.3-0.5-bifid;* segments occasionally incurved, often long apiculate, often with a uniseriate row of several cells, the segments terminating in a slime papilla, the segment margins entire; *margins of the lamina with 1-2(-3) small to large teeth*, rarely with 1 lacinium, the armature terminating in a slime papilla.

Plants dioecious; androecia terminal or intercalary on main axis or short to long lateral-intercalary branches (a single ventral-intercalary ♂ branch seen); bracts with basal portion strongly saccate, with apices appressed to bract immediately above; lobule margin involute, with several slime papillae and often few-celled teeth, or 1 lacinium, or 1 rounded involute lobe; antheridia solitary, stalk uniseriate.

FIG. 33. *Clasmatocolea gayana* (Mont.) Grolle.

Gynoecia on main axis or long lateral-intercalary branches; subfloral innovations when present (rare) originating from below bracts or bracteole of first or second series, usually lateral (1 ventral innovation seen); bracts in 3 series, those of innermost series usually free, rarely connate with keelar wing on 1 side, slightly concave, particularly in upper portion, obovate; apices undivided, broadly rounded or truncate, occasionally with 2 feebly developed, rounded lobes, the apex rather *densely denticulate with uni-*

seriate teeth; lamina margins sinuate, entire or sparingly denticulate in extreme upper portion, often with short, blunt projections of varying sizes. Bracteoles of innermost series subequal to bracts in size, free from bracts, concave or canaliculate (ventral view), especially in upper portion, margins in upper portion occasionally connivent, the bracteole ± appressed to the infolded ventral lobe of perianth, obovate; apices undivided or very short-bifid, broadly rounded, rather *densely denticulate;* lamina margins entire or sparingly denticulate in extreme upper portion, often with short, blunt projections of varying sizes. *Perianth nearly always present, strongly trigonous, subclavate to elongate-subrectangular to elliptic, the ventral side strongly infolded* lending perianth ± bilaterally compressed, the *perianth straight or gradually narrowing* toward the ± bilaterally compressed mouth; lobes broadly rounded or ± truncate, often with several short, blunt projections, *rather densely denticulate by teeth that are* (at least for a considerable portion distally) *uniseriate; keels with wings commonly large and conspicuous,* often dentate, occasionally sinuate, secondary wings occasional, of a few cells high.

Seta observed only in old, collapsed state. Capsule valves 0.83-0.91 mm. long, 34-42 μ thick, of 4-5 layers, the outer row of cells equal to thickness of ca. 2.3-2.5 of interior strata; outer layer with red-brown, wide nodule-like to wide spinelike thickenings that are often feebly tangentially dilated, a few semiannular bands present; exposed wall moderately thickened; intermediate and inner layers of cells subequal in thickness, the intermediate layers with thickenings often considerably tangentially dilated; inner layer of cells with red-brown semiannular bands, the bands often incomplete, sometimes branched, the radial walls with nodulose thickenings often present.

Spores 21-24 μ, red-brown, *exine with narrowly conical or subrectangular projections with dilated, flattened, or rounded tips* and with radiating bases interdigitating with one another, the intervening wall with weak nanogranules; spores *averaging 2.3 × elater diameter.* Elaters 10-12 μ wide, spiraled to tips, walls light brown.

Differentiation.—This species is one of the easiest of *Clasmatocolea* taxa to identify. Dried plants can be identified at once by the following ensemble of features: (a) the very commonly swollen apices and intercalary portions of axes; (b) the nearly strictly corticolous habit; (c) the very common presence of perianths; (d) the strongly incurved *apical portion* of leaves; and (e) the highly nitid plants. Upon wetting the plants the following combination of features is distinctive: (a) the dentate apical but more commonly dorsal leaf margins; (b) the underleaves that are connate on one side; (c) the presence of a raised, flat, disciform rhizoid initial field confluent with the median portion of the underleaf base; (d) the poorly differentiated stems, with cortical and medullary cells usually distinctly thick walled; (e) the rather densely denticulate bract apices, with the teeth uniseriate; (f) the rather densely denticulate perianth mouths, with the teeth uniseriate, at least for a considerable portion distally; and (g) the large, conspicuous, occasionally sinuate wings of the perianth keels.

Notes.—1. According to Schuster (1966), the presence of a well-defined rhizoid initial disc occurs primarily in Porellaceae, Frullaniaceae, and Lejeuneaceae. In *C. gayana,* this feature is a specialized one and is asso-

ciated with the corticolous habit of the species. Rhizoids may or may not issue from the rhizoid initial field.

2. Stephani (1900) described *Lophocolea concava* and listed Dusén material from Monte Tronador in Chile and Puerto Blest in Argentina, but the specimens from these localities bear no relationship to Stephani's description. Stephani (1906), in his treatment of *L. concava* in *Species Hepaticarum*, recognized the error and in effect typified the material by citing only Dusén material from Tierra del Fuego. *Lophocolea concava* is a synonym of *Leptoscyphus horizontalis* (*fide* Grolle, 1962). The material listed under *L. concava* in Stephani (1900) is actually *C. gayana* (*fide* material in S!). See also the discussion in Grolle (1962, pp. 43-44).

3. Pearson (1922) described a new species, *Conoscyphus flaccidus*, based upon a specimen collected in 1868 by Cunningham at Punta Arenas (Sandy Point), Chile, and named by Stephani as *Lophocolea humilis*. The outside of the packet of the holotype specimen (BM) neither bears the name *Conoscyphus flaccidus* nor an indication that Pearson saw the collection. However, within the packet there is a small blue slip of paper labeled "*Conoscyphus flaccidus* n. sp. Pearson M.S."

Ecology.—A corticolous species, for the most part in forests, occurring on *Nothofagus*, *Laurelia*, *Drimys*, *Saxegothaea*, *Araucaria*, *Weinmannia*, etc. Like *C. ctenophylla* it usually occurs where there is a minimal amount of competition with other bryophytes and commonly does not occur on trunks or branches covered with large, thick masses of bryophytes (which commonly frequent the very wet, west portions of southern South America). The species is sometimes intermixed with other hepatics such as *Lepicolea ochroleuca*, *Frullania* spp., *Metzgeria* spp., *Radula* sp., *Plagiochila* spp., *Porella subsquarrosa*, and *Clasmatocolea cucullistipula*. This species does not seem to be strictly altitudinally zoned, e.g., it occurs in Prov. Aisén (6-150 m.), Prov. Chiloé (near sea level-ca. 100 m.), Prov. Osorno (195-920 m.), Prov. Valdivia (10-1,000 m.), Prov. Cautín (730-800 m.), Prov. Malleco (330-1,280 m.).

Phytogeography.—Tierra del Fuego (sparse); Patagonian Channels; N. in Valdivian region (in West Patagonia N. to 37° 46′ S.; East Patagonia in Prov. Chubut and Prov. Río Negro). Hässel (1977) records the species for South Georgia; I have been unable to confirm or refute this report (see fig. 33).

Specimens seen.—**CHILE.** PROV. MAGALLANES: I. Ghebel, *Spegazzini 306* as syntype of *L. vinciguerrana* — c. per. (VER); I. Desolación, *Dusén s.n.* (S); ibid., Pto. Angosto, *Dusén 255* as *Leioscyphus turgescens* (LD), as *L. gayana* (NY, S); Brunswick Pen. (cf. Engel, 1978); E. side of B. Borja, *Engel 6135*, *6145* (MSC); I. Newton, *Dusén 17* (NY); Pto.

Charrúa, *Engel 4795* (MSC); Pto. Edén, *Engel 4554* — c. sporo. (MSC); SE point of I. Williams, *Engel 4473* (MSC). PROV. AISÉN: Pen. de Taitao, B. San Rafael, *Gusinde s.n.* — c. per. (JE); ibid., *Gusinde s.n.* as *L. puccioana* — c. per. (S); R. Aisén, *Dusén s.n.* as *L. humilis* (LD — c. sporo., O); ibid., *Dusén 230* as *L. humilis* — c. per. (JE); ibid., *Dusén 249* (NY — c. per., S — c. sporo.); Puerto Aisén, *Santesson M 318* as *L. puccioana* (S); 32 km. E. of Puerto Aisén, R. Aisén Valley, *Santesson M 326* (S); ibid., *Santesson M 327* as *L. puccioana* — c. per. (S); I. Magdalena, *Schwabe 20/1* — c. per. (JE); ibid., 6 m., *Schwabe 33/b* (hb. Grolle); Pto. Puyuhuapi, *Schwabe 4/b* — c. per., *8/a p.p.*, *8/e*, *23/b*, *23/d* — c. per. (JE); ibid., R. Obscuro, *Schwabe 21/a* (hb. Grolle); L. Risopatron, *Schwabe 6/c* (hb. Grolle). PROV. CHILOÉ: Pto. Ballena, *Engel 4225*, *4229* (MSC); I. Guaitecas, *Dusén 357* as *L. humilis* (S — c. per., UPS); ibid., Bo. Chica, *Dusén s.n.*, *368* as *L. humilis* (S); Melinca, *Dusén 357* as *L. humilis* — c. per. (S); I. Chiloé, Chadmo Central, just N. of Puente San Juan along Ruta 5, 20.9 km. by road N. of Quellon, ca. 50 m., *Engel 11960* (F); S. of Cucao near W. coast of I. Chiloé, C. Pirulil, 50 m., *Engel 12086* — c. per. (F); I. Chiloé, 1.3 km. by road N. of junction of Ruta 5 and road to Delcahue, ca. 100 m., *Engel 12158* (F); I. Chiloé, Lechagua area, 5 km. by road W. of Ancud, near sea level, *Engel 11712* — c. per. (F). PROV. LLANQUIHUE: Puerto Montt, *Claude Joseph 3203* as *L. ctenophylla* (MICH); ibid., Alerce, *Santesson M 557* — c. per. (S); Puerto Varas, *Dusén 461* — c. per. (FH, S). PROV. OSORNO: Antillanca, 920 m., *Ruthsatz 56/9* (hb. Grolle); Refugio Antillanca, 195 m., *Engel 3910B* (MSC); around L. Toro on road to Refugio Antillanca, 855 m., *Engel 4023* (MSC); near small lake 10.3 km. by road below Refugio Antillanca, 650 m., *Engel 11550* — c. per. (F); Agua Caliente, R. Chanleufú, 4 km. from Termas de Puyehue along road to Refugio Antillanca, 400 m., *Engel 11459* — c. per. (F); Termas de Puyehue, *Schwabe 64* (JE). PROV. OSORNO/PROV. VALDIVIA: Forest reserve at Planta Hydroeléctrica Pilmaiquén, along R. Pilmaiquén, 2 km. by road W. of Entre Lagos, ca. 100 m., *Engel 11597* (F). PROV. OSORNO near Prov. Valdivia boundary: Anticura, Salto del Indio, 19 km. by road E. of Termas de Puyehue along international highway, 300 m., *Engel 11664* — c. per. (F). PROV. VALDIVIA: W. slope of Cord. Pelada, W. of El Mirador, between La Union and Pta. Hueicolla, 580-840 m., *Engel 12273* — c. per., *12318* — c. per., *12345* — c. per. (F); E. slope of Cord. Pelada, E. of El Mirador, between La Union and Pta. Hueicolla, 740-840 m., *Engel 12422* — c. per., *12454* (F); Cord. Pelada, summit of El Mirador, between La Union and Pta. Hueicolla, 1,000 m., *Engel 12374* (F); Los Ulmos, *Mahu 7780* as *C. humilis* (hb. Grolle — c. per., hb. Mahu); E. slope near

R. Futa in vicinity of Futa, 10.5 km. by road S. of junction of highway T-60 and T-65, 10 m., *Engel 11019A* (F); V. Shoshuenco, *Ruthsatz s.n.* (JE); Corral, *Dusén 91* — c. per. (NY); ibid., *Krause s.n.* — c. per. (S); ibid. [Quitaluto], *Hosseus s.n.* — c. per. (PC); ibid., *Hosseus 657, 657B, 666, 667, 679 ex p.* — c. per. (JE); ibid., *Hosseus 662* — c. per., *668 p.p.* — c. per. (S); ibid., 430 m., *Hosseus 641, 643A* (JE); L. Riñihue, Enco, *Santesson M 673* — c. sporo., *M 677* — c. per., *M 679* — c. per., *M 680* — c. per., *M 682, M 686A* — c. per., *M 688* — c. sporo. as *L. puccioana* (S); Valdivia, *Herzog s.n.* as *L. puccioana* (JE); Arique, [? *Lechler*] (FH — c. per., NY, S). PROV. CAUTÍN: Termas de Palguín, R. Palguín, 730 m., *Engel 11334* — c. per., *11335* — c. per. (F); Parque Nac. Villarrica, N. slope of V. Villarrica, 800 m., *Engel 11202* — c. per., *11212* — c. per. (F); Pucón, V. Villarrica, *Hosseus 209* — c. per. (JE); ibid., *Hosseus 210A* (S). PROV. MALLECO: Cord. Nahuelbuta, Parque Nac. Contulmo, 7 km. by road E. of Contulmo, 330-360 m., *Engel 12537* (F). PROV. MALLECO/ PROV. ARAUCO: Cord. Nahuelbuta, Parque Nac. Nahuelbuta, 48 km. by road W. of Angol, 1,280 m., *Engel 12598* (F). **ARGENTINA.** PROV. CHUBUT: L. Puelo, *sin. coll. 11b* (JE). PROV. RÍO NEGRO: M. Tronador, *Dusén 577* as syntype of *Lophocolea concava* — c. sporo. (S); Puerto Blest, *Dusén 505* as syntype of *L. concava* — c. per. (S).

Clasmatocolea ctenophylla (Schiffn.) Grolle. Figures 34-35, Plates 15-16.

Lophocolea ctenophylla Schiffn. *in* Naumann, Forschungsr. *Gazelle* 4 (4):12. *pl. 3, f. 25-28.* 1889. *Clasmatocolea ctenophylla* (Schiffn.) Grolle, Rev. Bryol. Lichénol. 29:71. 1960. Holotype: Chile, Prov. Magallanes, I. Desolación, B. Tuesday, 2 February 1876, *Naumann s. n.* (FH! — c. per.).

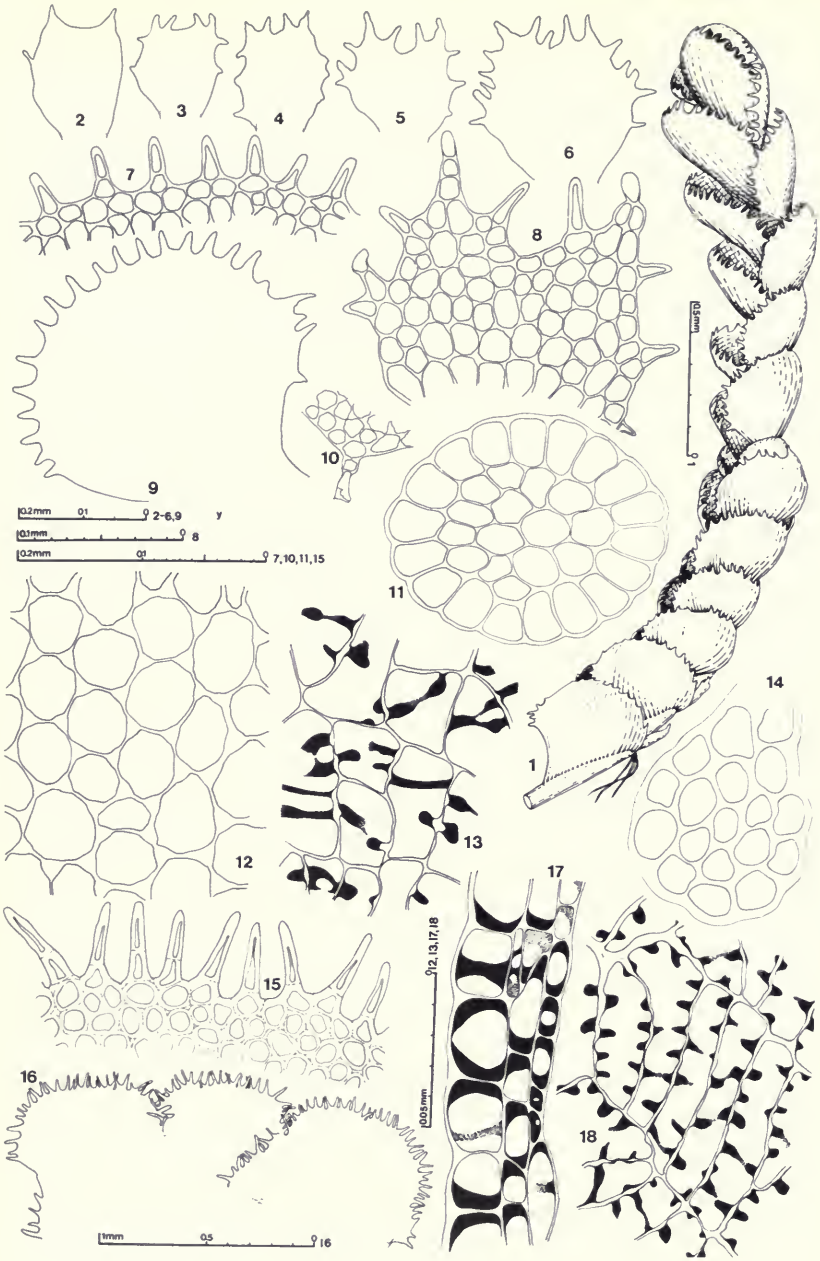
Lophocolea cristato-spinosa Steph. Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26 (III, 6):37. 1900, *syn. nov.* Original material: Chile, Prov. Llanquihue/Prov. Osorno, L. Llanquihue, *Dusén* (BM!, FH! — c. per., LD! — c. sporo., NY! — c. per.).

Plants *delicate*, prostrate, mixed with other bryophytes or pure in loose or dense, compact mats, *light green to pale grey-green, 315-490 μ wide.*

Branches frequent, sometimes copiously developed, *commonly of lateral-intercalary and* Frullania *types*, the former particularly common, *ventral-intercalary branches occasional.*

Stems (4-)5-6(-7) cells high, cortex in 1 row of distinctly thick-walled cells larger than medullary cells; medullary cell walls distinctly thickened; endophytic hyphae present in both cortex and medulla or absent. Rhizoids in fascicles from stem near underleaf base, long for plant size.

Leaves with insertion very slightly recurved at ventral end; leaves strongly erect, *the teeth of apical-dorsal portion intermeshing with those of opposite leaf;* leaves densely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0.2mm
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7,10,11,15
0.5mm
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12,13,17,18
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1mm
0.5
16

imbricate, conchiform concave, suboblate to wide-ovate; apex broadly rounded, undivided, often somewhat incurved; *apex and margins with 17-32 regularly spaced 1-2(-4)-celled sharp teeth that are ± equal in size; teeth with the tip cell usually thick-walled,* the tip cells of teeth toward base of dorsal margin often more elongated than other teeth; dorsal margin straight, *entire, or sparsely toothed in basal portion;* ventral margin broadly rounded.

Leaf cells thin to slightly thick-walled, trigones large and slightly to distinctly bulging, rarely medium; median leaf cells 17-26 μ wide, 18-26(-30) μ long; cuticle smooth, occasionally with some cells with smooth cuticle scattered among cells with roughened cuticle. Oil-bodies in all leaf cells except ultimate cells of teeth, occupying very small fraction of cell lumen, very light grey, of grape-cluster type, with numerous, small globules, the oil-body surface appearing finely botryoidal; oil-bodies variable: globose to ovoid to elliptic to crescentic in shape, consistently 2 per cell of middle, apex, or base of leaf, those of leaf middle 4-5 μ wide, 4-6 μ long.

Underleaves 1.4-2.1 × stem width, free, *appressed,* slightly convex (ventral view), *ovate to subrectangular, bifid to 0.20-0.33; segments often apiculate,* sometimes terminating in a slime papilla, the segment margins entire or with 1-2 sharp, thick-walled teeth near base of inner and/or outer margin; *margins of the lamina with several commonly 1-2-celled thick-walled teeth* that sometimes terminate in a slime papilla, the teeth occasionally somewhat larger, the margins rarely with only a few slime papillae.

Plants apparently dioecious; androecia not seen.

Gynoecia on main axis or short to rather long, lateral-intercalary branches; subfloral innovations absent or from below bract of first or second series; vestigial stem perigynium present; bracts in 3 series, the bracts and bracteole of innermost and second series inserted on stem perigynium; bracts of innermost series plane or slightly concave, obovate, insertion rather narrow; apices undivided, broadly rounded to truncate, *apex and margins of distal portion of lamina with numerous 1-2(-3)-celled thick-walled sharp teeth, the teeth subequal in size;* bracts entire toward base. Bracteoles of innermost series subequal to bracts in size, free from bracts; bracteoles canaliculate, usually appressed to the infolded ventral lobe of perianth, obovate to ± elliptic; the insertion sometimes rather narrow; apices variable: ± truncate, or narrowly rounded, or with 1 broadly triangular lobe, or with 2 small lobes and then retuse, the apex (plus lobes when present) and margins of distal portion of lamina *with teeth as in bracts;* bracteoles entire toward base. *Perianth strongly trigonous, subrectangular to narrowly ovate,* the ventral side convex or infolded, the distal portion of perianth ± bilaterally compressed,

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Opposite:

FIG. 34. *Clasmatocolea ctenophylla* (Schiffn.) Grolle. **1,** Portion of main axis, lateral-dorsal view. **2-6,** Underleaves. **7,** Teeth of apex and upper portion of ventral margin of leaf. **8,** Underleaf. **9,** Leaf (flattened). **10,** Portion of underleaf apex, tip a nearly collapsed slime papilla. **11,** Seta, cross section. **12,** Median leaf cells. **13,** Outer capsule wall cells. **14,** Stem, cross section. **15,** Perianth mouth. **16,** Perianth mouth, ventral lobe in middle. **17,** Capsule wall, cross section. **18,** Inner capsule wall cells with bands only sporadically represented. Figures 1-3, 7, 9, 10, 12, 14, 15, from holotype of *L. ctenophylla, Naumann,* Chile, Prov. Magallanes, B. Tuesday; figures 4, 11, 13, 16, from *Engel 4714,* Chile, Prov. Magallanes, I. Grant; figures 5, 8, from *Engel 4021A,* Chile, Prov. Osorno, L. Toro; figure 6, from *Engel 4240,* Chile, Prov. Chiloé, Pto. Ballena; figures 17, 18, from *Engel 5213,* Chile, Prov. Magallanes, I. Madre de Dios.

FIG. 35. *Clasmatocolea ctenophylla* (Schiffn.) Grolle. ○ = without specific location.

narrowing slightly in upper portion but expanding at immediate apex; perianth mouth ± bilaterally compressed, the lobes broadly rounded, *with numerous, 1-2-celled, thick-walled sharp teeth that are ± equal in size; keels often with large*, conspicuous, often very expanded, sometimes in part auriculate, *wings with numerous small teeth.*

Seta 5-6 cells in diameter, with 18 rows of outer thin-walled cells surrounding an inner core of scattered smaller cells with small trigone-like thickenings. Capsule valves 0.56-0.70 mm. long, 30-47 μ thick, of 3-4(-5) layers, the outer row of cells equal to thickness of 1.8-3 of interior strata; outer layer with red-brown, wide nodule-like or wide spinelike thickenings that are often weakly to strongly tangentially dilated, complete and incomplete semiannular bands common; exposed wall thin to moderately thickened; intermediate and inner layers of cells subequal in thickness, the intermediate layer(s) with thickenings often considerably extending onto tangential walls; inner layer of cells with red-brown semiannular bands very common on some valves, sporadic on others, often incomplete, the radial walls with nodulose thickenings very common on some valves, moderately represented on others.

Spores (11-)12-15 μ, light brown, *exine with ± hyaline, narrowly conical, rather widely spaced projections with often weakly dilated, often ± clawlike tips and with radiating bases*, the intervening wall has weak nanogranules; spores averaging 1.6 × elater diameter. Elaters (6-)7-9 μ wide, spiraled to tips or with apical portions with thick nonspiraled walls, elater walls red-brown.

Differentiation.—This small species should, even in the dried condition, offer no confusion with any other member of the genus. The following features will serve to identify it: (a) the corticolous habit; (b) the copious production of regularly shaped, ± equally sized, sharp, small teeth on the leaf margins; and (c) the small axis size (315-490 μ wide). The regular dentition and small axis stature lend a beautiful, intricate appearance to the plants. *Clasmatocolea ctenophylla* has spore ornamentation similar to two other corticolous taxa in the genus—*C. cucullistipula* and *C. gayana*—but the spores of *C. ctenophylla* differ in being ca. one-half the size.

Note.—At least one series of bracts and bracteoles of *C. ctenophylla* is inserted on a vestigial stem perigynium and in this species the phenomenon appears to be a response to fertilization.

Ecology.—A species of both deciduous and evergreen forests where corticolous on a variety of substrates—*Nothofagus pumilio*, *Drimys*, *Podocarpus*, etc., and occasionally on rotted logs and stumps. In the Valdivian region (near sea level-1,225 m.), it sometimes grows intermixed with *Xenocephalozia navicularis*, a species, in general, with a similar ecology. *Clasmatocolea ctenophylla* usually occurs where there is a minimal amount of competition with other bryophytes and commonly does *not* occur on those tree trunks that, in the range of this species, are so frequently covered with large, thick masses of bryophytes.

Phytogeography.—Tierra del Fuego (I. Grande de Tierra del Fuego and I. Desolación); Patagonian Channels; N. in Valdivian region to 39° 52′ S. (Corral, Prov. Valdivia) (see fig. 35).

Specimens seen.—**CHILE.** PROV. MAGALLANES: Ens. Villarino, *Hatcher 52b* (NY); I. Desolación, *Dusén s.n.* (FH); ibid., Pto. Angusto, *Dusén 417* as *L. gayana* (S); I. Desolación, Pto. Churruca, head of Br. Lobo, *Engel 5813* — c. per. (MSC); I. Desolación, B. Tuesday, head of inner harbor, *Engel 5701* (MSC); S. side of I. Madre de Dios, N. of I. Tarlton, *Engel 5213* — c. sporo., *5214* — c. per. (MSC); W. side of I. Grant, *Engel 4714* — c. sporo. (MSC). PROV. AISÉN: I. Magdalena, *Schwabe 33/b 2 p.p.* as *L. multispinula* (JE). PROV. CHILOÉ: Pto. Ballena, *Engel 4240* (MSC); I. Guaitecas, Melinca, *Dusén 417* as *L. gayana* (NY); I. Chiloé, Cord. San Pedro, Butalcura, near R. Butalcura, 11 km. by road from Ruta 5, 100 m., *Engel 11831* (F); I. Chiloé, Aguas Buenas area, 4.7 km. E. along Aguas Buenas road from Ancud-Quemchi road, ca. 100 m., *Engel 12212* (F); I. Chiloé, Chepu, S. side of R. Chepu, near sea level, *Engel 11735*, *11764* (F). PROV. OSORNO: Antillanca, (?) 1,225 m., *Ruthsatz 58/4* (hb. Grolle); around L. Toro on road to Refugio Antillanca, 855 m., *Engel 4021A* (MSC); 12.1 km. by road below Refugio Antillanca, 550 m., *Engel 11543A* (F). PROV. VALDIVIA: W. slope of Cord. Pelada, W. of El Mirador, between La Union and Pta. Hueicolla, 580 m., *Engel 12288* — c. per. (F); E. slope of Cord. Pelada, E. of El Mirador, between La Union and Pta. Hueicolla, 840 m., *Engel 12407* (F); Corral [Quitaluto], *Hosseus 116* (hb. Grolle, JE).

Clasmatocolea crassiretis (Herz.) Grolle. Figures 36-37.

Lophocolea crassiretis Herz. Trans. & Proc. Roy. Soc. New Zealand 65:354. 1935. *Clasmatocolea crassiretis* (Herz.) Grolle, Nova Acta Leop. 25 (161):69. 1962. Holotype: New Zealand, North Island, Te Matawai, Tararuas, 3 June 1932, *Zotov 135* (JE! — c. per.; isotypes: CHR!, JE!).

Plants *rigid*, prostrate, in nearly pure mats or mixed with other bryophytes, *yellow brown to light brown, highly nitid when dry, submoniliform* (especially in ventral view); *axes 0.5-0.6 mm. wide.*

Branches sporadic, *lateral-intercalary type common*, from near ventral end of merophyte, *ventral-intercalary type sporadic, terminal branching absent.*

Stems slender for plant size, rigid, wiry, frequently arced or wavy, commonly not growing straight, *5-6 cells high, cortex in 1 layer of thick-walled cells larger than the medullary cells*, the outer tangential wall very thickened; *medullary cell walls thick;* endophytic hyphae present in both cortex and medulla. Rhizoids occasionally present, in tight fascicles from stem at underleaf bases.

Leaves rather fragile, the insertion slightly recurved at ventral end; leaves strongly erect, opposing leaves connivent or closely approaching, the axis appearing ± narrowly channeled in dorsal view, the leaves imbricate, deeply conchiform concave, *appearing inflated and billowed out*, orbicular to oblate, the apex broadly rounded, undivided, *the apex and margins entire;* dorsal margin ± straight in proximal portion, the distal

FIG. 36. *Clasmatocolea crassiretis* (Herz.) Grolle. **1,** Axis, dorsal-lateral view. **2,** Portion of axis, lateral view. **3,** Perianth bearing axis, lateral view. **4, 5,** Adaxial and abaxial views of same leaf. **6,** Apex of gynoecial shoot, ventral view. **7,** Portion of main axis, ventral view. **8,** Antheridial stalk. **9,** Median leaf cells. **10,** Stem, cross section. **11-18,** Underleaves, in situ. Figures 1-5, 7, 9-16, 18, from holotype, *Zotov 135*, New Zealand, North I., Tararuas; figure 6, from isotype (JE); figure 8, from *Druce s.n.*, New Zealand, North I., Maungapohatu; figure 17, from *Scott s.n.*, New Zealand, Stewart I., Mt. Anglem Track.

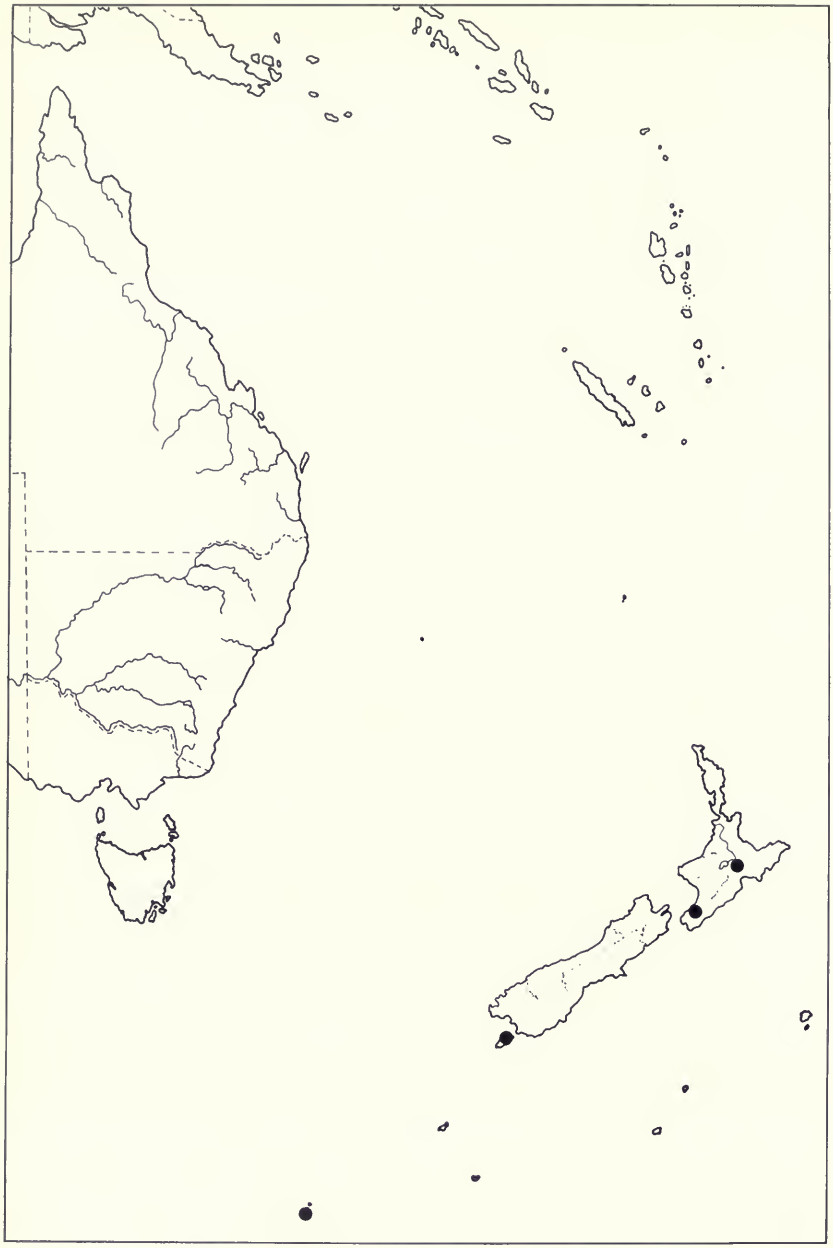


FIG. 37. *Clasmatocolea crassiretis* (Herz.) Grolle.

portion broadly rounded, the margin slightly undulate, decurrent; ventral margin broadly rounded, *the basal portion subauriculate and conspicuously extending ventrally beyond stem.*

Leaf cells with massive, nodular, or maximally protuberant, irregularly triangular to rectangular trigones that are confluent or separated by narrow thin-walled places, the cell lumen bounded mostly by the massive trigones; median leaf cells 13-20(-24) μ wide, (16-)18-26 μ long; *cuticle smooth.*

Underleaves rigid, 0.9-1.3 × stem width, often asymmetrically oriented, free, strongly spreading, sometimes diverging from axis at 90°, distant, sometimes partially obscured by ventral portion of adjacent leaf, *plane, cuneate to suborbicular to oblate to ovate; apices undivided, truncate to emarginate,* commonly with a pair of slime papillae; *margins of the lamina entire* except for an occasional slime papilla.

Plants dioecious; androecia intercalary on main axis, bracts densely imbricate and with apices usually appressed to bract immediately above, the bracts considerably smaller than leaves, deeply concave and strongly saccate at the base; lobule abbreviated, the margin slightly inflexed, broadly rounded, entire; antheridia solitary, stalk uniseriate.

Gynoecia on leading axes or short to long lateral-intercalary branches; subfloral innovations absent; bracts in 2-3 series, the bracts of innermost series with insertion rather narrow, the bracts erect and appressed (or nearly so) to the perianth, deeply conchiform concave, rotundate to ovate, apices and margins broadly rounded, entire. Bracteoles of innermost series free from bracts, plane, *partially obscured by bracts,* cuneate to elliptic, apices broadly rounded (and sometimes repand) to shallowly emarginate to bidentate, entire. *Perianth inflated, terete, cylindrical to clavate to elliptical* (young perianths frequently campanulate), the sides slightly narrowing or straight or moderately expanding toward the mouth, the mouth wide and open or partially closed by incurving of some or all of lobes; lobes free for 0.15-0.25 perianth length, the dorsal lobes broadly rounded, occasionally incurved, *entire, the ventral lobe distinctly smaller,* narrowly rounded, incurved, *entire; keels absent, wings usually absent* (only one seen).

Sporophyte not seen.

Differentiation.—This species is quite comparable to *C. strongylophylla* (*C. turgescens*), which also occurs in New Zealand, in (a) general aspect and small stature of the plants; (b) underleaf shape variability; (c) general shape of the inflated perianths, including the smaller, incurved ventral lobe; and (d) the broadly rounded, slightly incurved and entire male bract lobules. In fact, these characters serve to indicate that sections *Clasmatocolea* and *Strongylophyllae* are allied and related through *C. strongylophylla* and *C. crassiretis.*

Clasmatocolea crassiretis and *C. strongylophylla* should, however, not be confused and may be separated as follows:

Character	C. crassiretis	C. strongylophylla
Leaf cuticle	Smooth	Coarsely papillate
Leaf trigones	Massive, protuberent	Large to bulging
Underleaves	Strongly and stiffly spreading, undivided	Appressed to moderately spreading, commonly divided

Character	C. crassiretis	C. strongylophylla
Branching	Strictly intercalary	Mostly terminal, occasionally intercalary
Perianths	Usually smooth, not winged	Winged

The closest ally of *C. crassiretis* appears to be *C. humilis* var. *humilis*. The two are separable as follows (note that several of the characters are qualitative):

Character	C. crassiretis	C. humilis var. humilis
Underleaves	To 1.3 × stem width, free, plane and not convex (ventral view), undivided, never bifid	To 4.3 × stem width, free or connate on 1 side, slightly to deeply convex (ventral view), sometimes cupulate, bifid or undivided
Branching	Terminal absent, mostly lateral-intercalary	Mostly ventral- and lateral-intercalary, terminal occasional
Leaf cells	Trigones massive, protuberant; leaf cell lumen bounded mostly by the massive trigones	Trigones large to bulging to knotlike; leaf cell lumen bounded mostly by cell wall
Stem	5-6 cells high	8-14 cells high
Perianth	Inflated, terete, the ventral side not infolded; wings rare	Strongly trigonous, the ventral side usually strongly infolded; wings common
Plant size	Smaller, to 0.6 mm. wide	Larger, to 1.8 mm. wide
Habitat	Often corticolous	Terricolous, saxicolous, or on rotted logs

Ecology-Phytogeography.—Usually corticolous in *Olearia* scrub or wet, mossy, *Dracophyllum biforme-Olearia* forests where associated with *Plagiochila pleurota* and *Goebeliella cornigera;* very rarely on ground. Known from Macquarie Is.; Stewart I. (535-790 m.) and North I. (885-1,530 m.), New Zealand (see fig. 37).

Specimens seen.—**MACQUARIE IS.:** *Ashton s.n.* (hb. Grolle). **NEW ZEALAND. STEWART I.:** Mt. Anglem Track, 790 m., *Mork s.n.* as *C. turgescens* (CHR); ibid., 535 m., *Scott* as *C. turgescens* — c. per. (hb. Child, F); Mt. Anglem Track, *Scott* as *C. turgescens* (CHR). **NORTH ISLAND.** WELLINGTON: Schormann's Track, E. slopes of Mt. Hines, N. Tararua Mts., 10-12 mi. W. of Eketahuna, 885-1,005 m., *Schuster 49174a* — c. per. (hb. Schuster); ibid., *Schuster 49160, 49167A* (F, hb. Schuster). GISBORNE: Maungapohatu, Urewera, 1,530 m., *Druce s.n.* — c. ♂ (hb. Grolle).

Clasmatocolea moniliformis Engel. Figures 38, 39.

Clasmatocolea moniliformis Engel, Phytologia 41:310. 1979. Holotype: Chile, Prov. Magallanes, E. side of B. Borja, *Engel 6159* (MSC!).

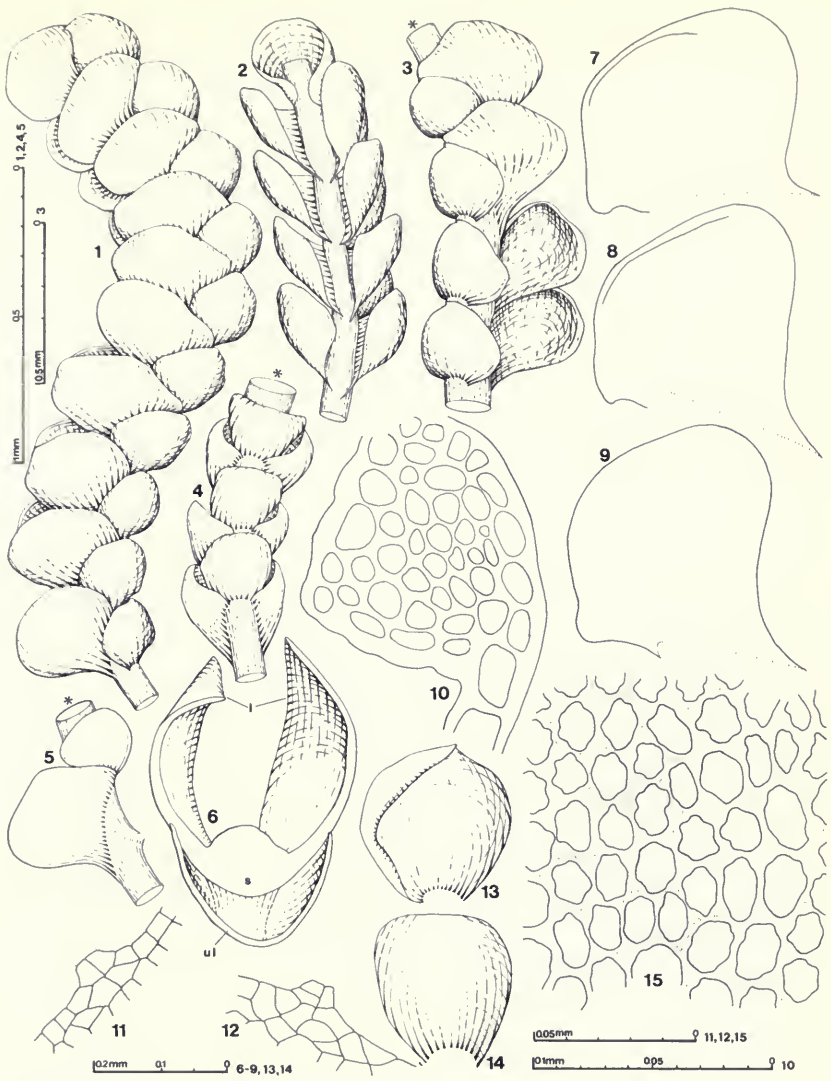


FIG. 38. *Clasmatocolea moniliformis* Engel. **1,** Main axis, lateral view. **2,** Axis, dorsal view, with apical pair of leaves removed to show underleaves. **3,** Axis, lateral view, with 2 basal leaves removed on 1 side. **4,** Portion of axis showing leaf and underleaf insertion, ventral view. **5,** Leaf and underleaf, lateral view. **6,** Axis, cross section (l = leaves; ul = underleaves; s = stem). **7-9,** Leaves; note ventral-basal subauriculate projections. **10,** Stem, cross section. **11, 12,** Stalked slime papillae of underleaf apex. **13, 14,** Underleaves, lateral and ventral views. **15,** Median leaf cells. Figures 1-5, 9-15, from holotype; figures 6, 8, from *Engel 6231*, Chile, Prov. Magallanes, B. Borja; figure 7, from *Engel 5677*, Chile, Prov. Magallanes, B. Tuesday.

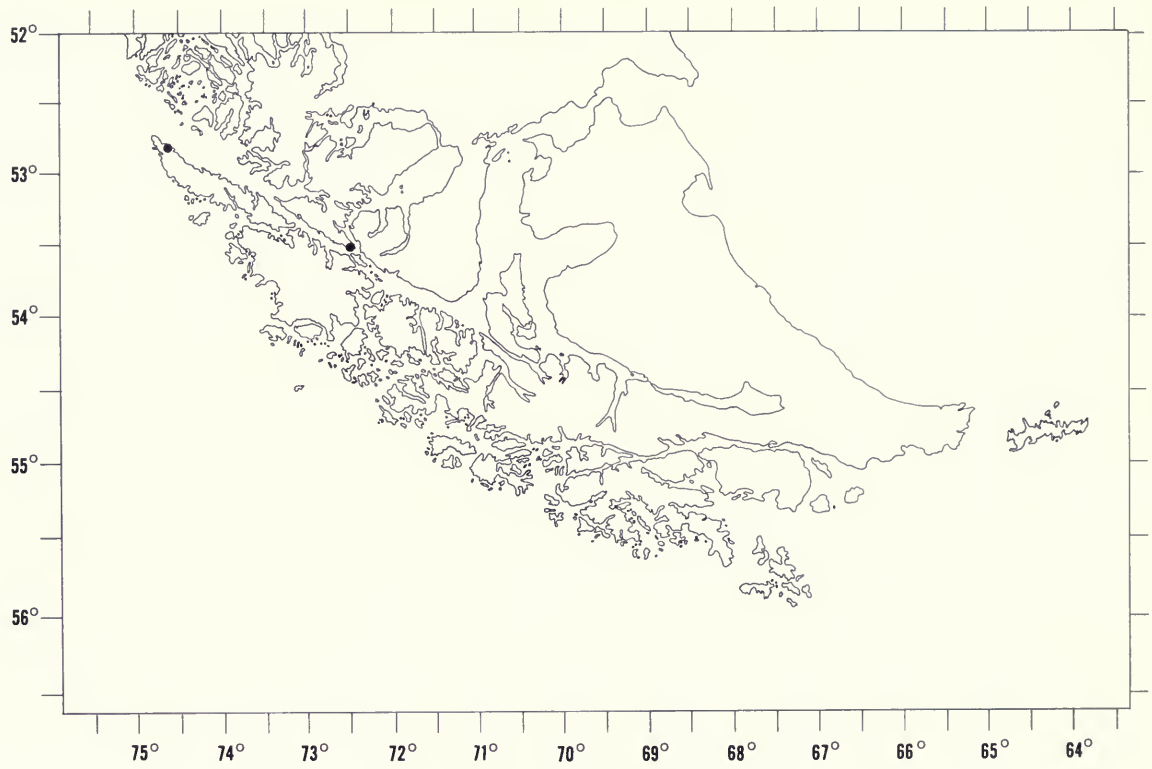


FIG. 39. *Clasmatocolea moniliformis* Engel.

Plants *rigid, fragile*, prostrate, in nearly pure mats or more often mixed with other bryophytes, *golden brown*, nitid when dry, *capillaceous, distinctly moniliform; axes 315-420 μ wide.*

Branches rather frequent, *nearly exclusively of ventral-intercalary type, lateral-intercalary type absent*, Frullania-*type very rare* (only 1 branch seen).

Stems brittle, frequently arced or wavy, commonly not growing straight, 6-9 cells high, *with little internal differentiation*, the cortex in 1-2 rows of thick-walled cells slightly larger than, about the same size as, or slightly smaller than the medullary cells, the outer tangential wall very thickened; medullary cell walls thick. Rhizoids not seen.

Leaves usually with marginal 1-3 hyaline cell rows, insertion not recurved at ventral end, the ventral end of leaf inserted on stem at immediate base of underleaf or on basal few cells of underleaf lamina; leaves erect but not connivent, the axis appearing channeled in dorsal view, the leaves imbricate, distinctly concave, producing a sharp, elongate bulge in lateral view, the distal portion of the leaf moderately incurved; *leaves subsquarrose, with the dorsal portion of the otherwise obliquely truncate, undivided apex rather narrowly rounded, the sides of the leaf ± parallel, the margins and apices entire; dorsal margin ± straight*, plane, *long decurrent; ventral margin ± straight*, considerably shorter than the dorsal margin, the *extreme base of ventral margin slightly broadened and forming a subauriculate projection that sharply narrows toward the insertion, the ventral-basal portion of leaf sheathing marginal parts of the underleaf base.*

Leaf cells distinctly thick walled, trigones large, often bulging and often confluent; median leaf cells 11-14(-17) μ wide, 14-22 μ long; basal cells very thick walled and more deeply pigmented; cuticle smooth. Oil-bodies throughout leaf *except in marginal 1-2 rows, obscuring ca. 0.20-0.75 of cell lumen*, very light grey or off-white, of grape-cluster type, the oil-body *surface appearing coarsely granular;* oil-bodies subglobose to ovoid to elliptic in shape, occasionally somewhat irregular, 2-3 per cell of leaf middle and base, 1-2(-3) of leaf apex, those of leaf middle 3-5 μ wide, (3-)5-6(-8) μ long; oil-bodies of underleaf 1-3(-4) per cell, of same size as those of leaf middle.

Underleaves 4.6-6.7 × stem width, free or *base of underleaf lamina connate with leaf on 1 side, the underleaves with apical portion appressed to stem;* underleaves approximate to contiguous, *cucullate, inflated, billowed out*, frequently containing miscellaneous debris, *clasping stem, the margins curved dorsally and extending above dorsal stem surface; apices undivided*, broadly rounded or truncate, slightly reflexed, *entire*, but with a few, commonly short-stalked slime papillae; *margins of the lamina entire* except for an occasional slime papilla.

Androecia and gynoecia not seen.

Differentiation.—This species stands quite isolated in Sect. *Clasmatocolea*, because of the following ensemble of features:

1) The leaf insertion does not recurve at the ventral end; the ventral ends of a pair of opposing leaves are inserted on the stem in very close proximity to the underleaf or may sometimes be inserted, on one side, on the basal few cells of the underleaf *lamina*. Because of this kind of leaf insertion, coupled with the ventral-basal subauriculate projections of the leaves, the basal-lateral portion of the underleaves are sheathed on both sides by leaf tissue.

2) Branching in *C. moniliformis* is unique to the section, for in this

species branches are nearly exclusively ventral-intercalary (only a single *Frullania*-type branch was seen, and lateral-intercalary branches are absent).

3) The cucullate underleaves represent an extreme condition within the section, being only somewhat approached by some forms of *C. humilis*. In such plants of *C. humilis*, however, the underleaf apices are not closely appressed to the stem and are less than 4.8 × the stem width.

4) The distinctly moniliform appearance of the axes is unique to the section.

Of the members of Sect. *Clasmatocolea*, the closest relative appears to be *C. humilis*. Differences in axis size, branching modalities, leaf insertion, and underleaves will distinguish these taxa.

Clasmatocolea moniliformis shows some relationships to the New Zealand *C. crassiretis*, which also consists of small, stiff plants with brownish pigments and strictly intercalary branching. Differences in underleaves and branching modalities will easily separate these plants.

Clasmatocolea moniliformis may possibly be confused with the rather distantly related *C. cucullistipula*, which has the same general stature and appearance. The two taxa are separable as follows:

Character	C. cucullistipula	C. moniliformis
Leaf margins	1-4-dentate	Entire
Underleaf margin	With one large lobe	Entire
Underleaf base	Subauriculate	Narrowing toward the base; not auriculate
Branching	*Frullania*-type predominant; ventral-intercalary occasional	Ventral intercalary; *Frullania*-type very rare
Color	Light olive green-light brown	Golden brown
Habit	Corticolous	Saxicolous

Ecology-Phytogeography.—Only in the cold, very wet southernmost channel region (S. of ca. 53° 30′ S. in Prov. Magallanes), in both forests as well as exposed outcrops and moorland areas. The species is saxicolous, especially where there has been an accumulation of soil and where a layer of bryophytes is present. It is frequently mixed with other hepatics such as *Cryptochila* sp., *Grollea*, *Krunodiplophyllum squarrosum*, *Metahygrobiella* sp., *Pachyglossa* sp., *Pleurocladopsis simulans*, and *Riccardia* sp. (see fig. 39).

Specimens seen.—**CHILE.** PROV. MAGALLANES: I. Desolación, B. Tuesday, head of inner harbor, *Engel 5677*, *5778C* (MSC); E. side of B. Borja, *Engel 6188*, *6216C*, *6231* (MSC).

Clasmatocolea minutiretis Engel & Grolle. Figures 40-42, Plates 17, 18.

Clasmatocolea minutiretis Engel & Grolle *in* Engel, Phytologia 41:309. 1979. Holotype: Chile, Prov. Magallanes, E. shore of I. Pilot, *Engel 4785* — c. sporo. + ♂ (MSC!).

Plants rather soft, but with stiff, wirelike stems, suberect, the plants in dense, pure, compact mats, *pale brown to pale reddish brown*, the *stems a rich red-brown*, the leaves pale red-brown above, but with a well-defined strip of red-brown pigmentation near the insertion, in ventral view the leaves with a small, local, concentrated patch of red-brown pigment at the ventral-basal point of insertion, the leaves often mottled with patches of red-brown; axes to 1.4 mm. wide, *often with a somewhat inflated appearance in ventral view*, the axes often with several separated, intercalary, swollen and/or diminutive areas; axis apices becoming long attenuated, with reduced but imbricate leaves, the apices sometimes becoming subflagelliform.

Branches abundant, sometimes arising from a mass of entangled, old, dead, leafless axes, the *ventral-intercalary type very common*, *lateral-intercalary occasional*, *terminal branches absent*.

Stems 7-8 cells high, *cortex very thick-walled*, *not markedly differentiated*, in a single row of red-brown pigmented cells with walls slightly thicker than those of the medullary; *medullary cells very thick-walled*. Rhizoids sporadically developed, in dense fascicles from a rather wide field at the underleaf bases.

Leaves with insertion oblique, very slightly recurved at ventral end; leaves strongly erect and connivent or nearly so on robust axes, those on less well-developed shoots either suberect but not connivent (and then with the axis appearing narrowly channeled in dorsal view) or with the leaves moderately to distinctly spreading; leaves rather closely imbricate, deeply conchiform concave, *the ventral-basal portion appearing billowed out and extending ventrally well beyond stem surface*, *the ventral-basal portion often extending laterally and overlapping the ventral-basal region of opposing leaf and thereby often partially or totally obscuring view of both stem and underleaves;* leaves orbicular to wide-ovate to oblate; apex often slightly undulate, broadly rounded to subtruncate, undivided, *the apex and ventral margin with several irregularly sized and spaced*, *often incurved teeth* along with low, rounded projections, *the dorsal margin entire;* dorsal margin ± straight proximally, moderately rounded distally, the two areas often separated by a rather sharp, humplike projection that generally occurs in the median portion of the margin, the dorsal margin plane or slightly undulate, short decurrent; ventral margin broadly rounded, *incurved toward the base and thus accentuating the sharply defined leaf concavity*.

Leaf cells *somewhat thick-walled*, *trigones large to knotlike;* median leaf cells 14-24 μ wide, 19-30 μ long; cuticle smooth.

Underleaves reduced and rather inconspicuous but distinct and persistent, on robust axes frequently partially or wholly hidden by ventral portion of adjacent leaves, *0.35-0.6 × stem width*, *free*, *but in close proximity to leaf on one side; underleaves loosely appressed or more often slightly spreading*, distant, plane, or slightly convex (ventral view), *narrowly lanceolate to narrowly long-triangular*, *bifid to 0.55-0.7*, but in less robust axes with lamina of only 1-2 cells high and then underleaves divided nearly to base; *segments cilia-like*, straight or flexuous, *with a uniseriate portion of up to 7(-9) cells originating from a base 2 cells wide*, the segments sometimes uniseriate throughout;

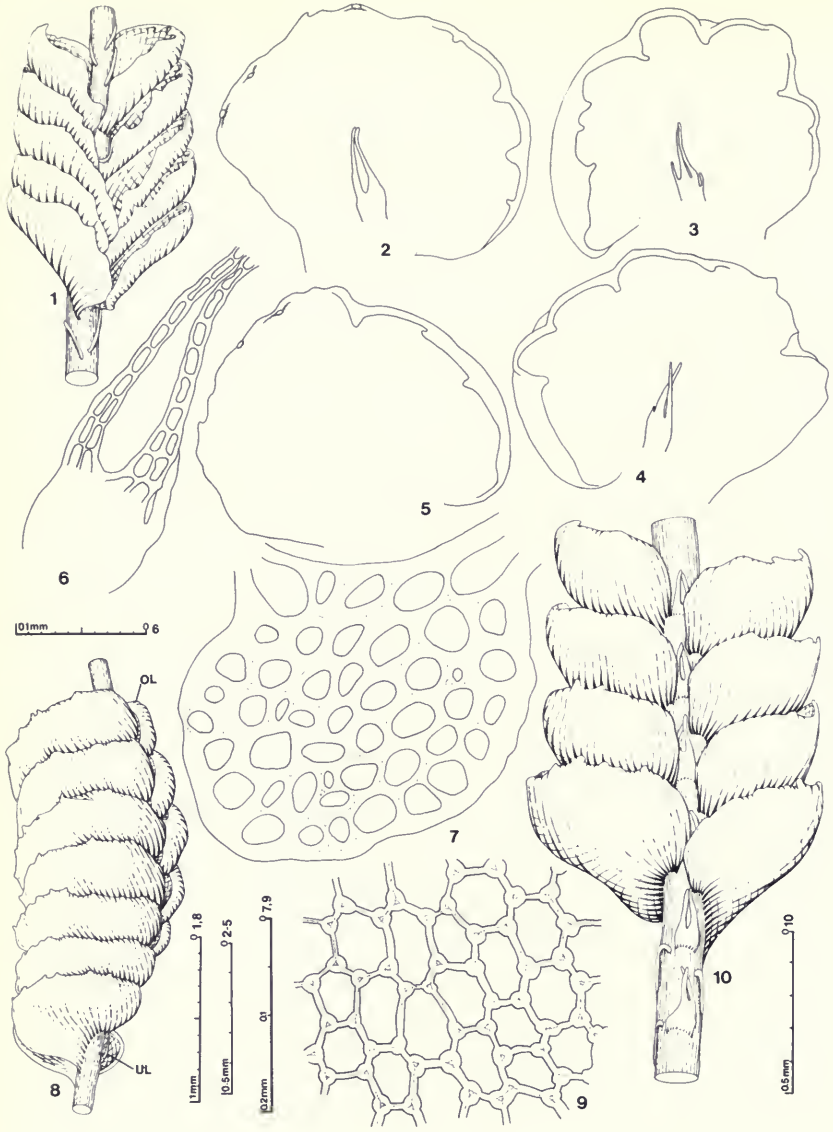


FIG. 40. *Clasmatocolea minutiretis* Engel & Grolle. **1,** Portion of axis, dorsal view. **2-5,** Leaves and within, underleaves. **6,** Underleaf. **7,** Stem, cross section. **8,** Portion of axis, lateral view; note underleaf (UL), and saccate ventral portion of opposing leaves (OL) toward axis apex. **9,** Median leaf cells. **10,** Portion of axis, ventral view. All from holotype.

FIG. 41. *Clasmatocotea minutiretis* Engel & Grolle. **1,** Gynoecium, ventral view. **2,** Perianth mouth, ventral lobe in middle. **3,** Seta, cross section. **4,** Inner capsule wall cells. **5,** Outer capsule wall cells. **6,** Diagrammatic representation of branching pattern. **7,** Capsule wall, cross section. **8,** Antheridial stalk. **9,** Opposing antheridial bracts with stem (S), cross section. **10,** Male bract. All from holotype.

FIG. 42. *Clasmatocolea minutiretis* Engel & Grolle. Plus Tristan da Cunha.

segments terminating in a slime papilla, the segment margins entire; *margins of the lamina entire or with 1* short or long and ciliform *tooth.*

Plants dioecious; androecia terminal or intercalary on leading axes; *bracts obliterating or nearly so the view of dorsal stem surface*, the bracts with basal portion strongly saccate, *the saccate portion fused toward base with opposite bract*, the distal portion strongly concave, with apices appressed to bract immediately above, the lobe margins with several teeth; lobule margin incurved, irregularly broadly rounded, with a few low, rounded projections and slime papillae; antheridia solitary, stalk uniseriate.

Gynoecia on leading axes or rather short branches as well as subfloral innovations; vestigial stem perigynium present; bracts and bracteoles in 3 series, those of the innermost series inserted on the stem perigynium; bracts of innermost series plane or slightly concave, orbicular to obovate; apices broadly rounded, undulate, with several coarse teeth and laciniae, the armature often sharply incurved; dorsal margin entire proximally, repand or more often armed with a few teeth and laciniae distally, the margin straight or arcing toward the perianth, plane or becoming undulate distally in area of armature; ventral margin much like that of the dorsal. Bracteoles of innermost series free from bracts, rather strongly concave (ventral view), narrowly to broadly obovate, sometimes orbicular; apices bifid to ca. 0.25, less often emarginate, the segments occasionally canaliculate; lamina margins entire in proximal portion, the distal portion armed with a few, often recurved teeth or laciniae, the margins sharply recurved (curved ventrally), sometimes undulate distally. *Perianth strongly trigonous*, elongate-subrectangular to narrowly subclavate, not or barely narrowing toward the small or ± closed mouth; lobes broadly rounded, sometimes incurved, the ventral lobe and 1 or both side lobes infolded, *the lobes coarsely armed with sharp or rounded teeth;* keels occasionally with wings of a few cells high.

Seta 7-8 cells in diameter, with 19-20 rows of outer cells with corners thickened similar to medium-large trigones; inner core cells scattered, smaller than outer row, with corners thickened similar to small to medium trigones. Capsule elliptic, the valves 0.75-0.84 mm. long, 30-34 μ thick, of 3-5 layers, *the outer layer of cells exceeding thickness of all interior strata combined;* outer layer with red-brown, nodule-like or weakly spinelike thickenings that are often feebly tangentially dilated, a few *semiannular bands present;* exposed wall thickened; intermediate and inner layers of cells subequal in thickness, the intermediate layers with thickenings, often feebly tangentially dilated; inner layer of cells with red-brown semiannular bands common, the bands often incomplete, the radial walls with nodular thickenings very common.

Spores 12-13 μ, light brown, spherical or subspherical, exine with the light microscope appearing minutely punctuate, but under the SEM with granulate to short, irregular, wide vermiform projections that have nanogranules, the intervening hollows with nanogranules; *spores averaging 1.2 × elater diameter.* Elaters 8-10 μ wide, apical portions occasionally with thick nonspiral walls; elater walls red-brown, 2-3 μ in diameter.

Differentiation.—Clasmatocolea minutiretis bears definite affinities to *C. humilis*, yet must remain an isolated element within Sect. *Clasmatocolea.* With *C. humilis*, *C. minutiretis* shares such features as leaf form, cell size, and trigone characters, predominance of intercalary branching (but in *C. minutiretis*, branching is strictly intercalary, just as in *C. crassiretis* and, practically, *C. moniliformis* of the same section), and spore size and

surface features. Two features, however, rather isolate *C. minutiretis* in the section.

First, underleaves represent an extreme form of reduction, being quite inconspicuous and 0.35-0.6 × the stem width. The underleaves of this species represent the culmination of an interesting trend in the section, from large, robust structures in *C. moniliformis* (here to 6.7 × stem width) and *C. humilis* var. *humilis* to those of *C. humilis* subsp. *polymorpha* to *C. vermicularis*, and finally, with a considerable reduction in magnitude, to *C. minutiretis*.

Second, opposing male bracts are fused toward the base, a feature occurring only in *C. trachyopa* and *C. obvoluta* of the quite unrelated Subg. *Lacerifolia*.

In dorsal aspect, plants of *C. minutiretis* resemble *C. humilis* var. *suspecta* quite closely. A ventral view will immediately distinguish *C. minutiretis*, with its reduced, inconspicuous underleaves that are at most 0.6 × the stem width and bifid to 0.55-0.7.

At first glance, *C. minutiretis* brings to mind *C. navistipula* var. *navistipula* in general aspect of the plants, and in the reduced, inconspicuous underleaves and profuse branching (see fig. 53). However, I regard the similarity of the taxa as a superficial one and believe *C. minutiretis* belongs, more naturally, in Sect. *Clasmatocolea*.

Ecology.—Over rock in mossy forests or shaded, rocky stream valleys; sometimes mixed with *C. humilis*, less often with *C. trachyopa*.

Phytogeography.—Tristan da Cunha and southern South America, occurring at ca. 50° 00-20′S. in Prov. Magallanes and in Prov. Neuquén, Argentina (1,500 m.) (see fig. 42).

Specimens seen.—**TRISTAN DA CUNHA:** Above Burntwood, *Christophersen & Mejland 803* (hb. Grolle). **CHILE.** PROV. MAGALLANES: S. side of I. Madre de Dios, head of fiord E. of M. Roberto, *Engel 5123*, *5129B*, *5156* (MSC); E. shore of I. Pilot, *Engel 4750* — c. per., *4770* — c. sporo. + ♂ (MSC). **ARGENTINA.** PROV. RÍO NEGRO: Parque Nac. Nahuel Huapí, [M.] Tronador, 1,500 m., *Donat 182* (mixed with holotype of *L. catenulata* = *C. humilis*) (hb. Grolle, JE).

Sect. **FULVELLAE** Engel, sect. nov.

Rami intercalares plane dissimiles quam principale axe, vermiformes et submoniliformes, angustiores quam principale axe, plerumque copiosi, et breves, abbreviati, habentes amphigastria imbricata propinquioria quam illis principale axe; amphigastria rami intercalaris grandia, orbicularia, valde cupulata, inflata, plerumque indivisa; folia caulina principalis axis sinuata ac incurvata, plerumque habentia aliquot grandium dentium et laciniarum.

Type species: *Clasmatocolea fulvella* (Hook. f. & Tayl.) Grolle.

Intercalary branches quite different from main axis, the branches vermiform and submoniliform, narrower in width than main axis, commonly copiously produced and short, abbreviated, with underleaves more closely imbricate than underleaves of main axis; intercalary branch underleaves large, orbicular, distinctly cupulate, appearing inflated, usually undivided; leaves of main axis sinuous and incurved, usually with a few large teeth and laciniae; underleaves of main axis ± cupulate, the apical portion commonly either approaching or in contact with stem, the basal portion abruptly convex (ventral view).

Distribution.—Southern South America and Falkland Is.

Clasmatocolea fulvella (Hook. f. & Tayl.) Grolle. Figures 43-45, Plates 19, 20.

Jungermannia fulvella Hook. f. & Tayl. London J. Bot. 3:464. 1844. *Chiloscyphus fulvellus* (Hook. f. & Tayl.) Nees *in* G. L. & N. Syn. Hep. 711. 1847. *Lophocolea fulvella* (Hook. f. & Tayl.) Mass. Nuovo Giorn. Bot. Ital. I. 17:227. 1885. *Clasmatocolea fulvella* (Hook. f. & Tayl.) Grolle, Rev. Bryol. Lichénol. 29:72. 1960. Lectotype (*nov.*): Chile, Prov. Magallanes, I. Hermite, *Hooker s.n.* (FH! — c. per. + sporo. + ♂).

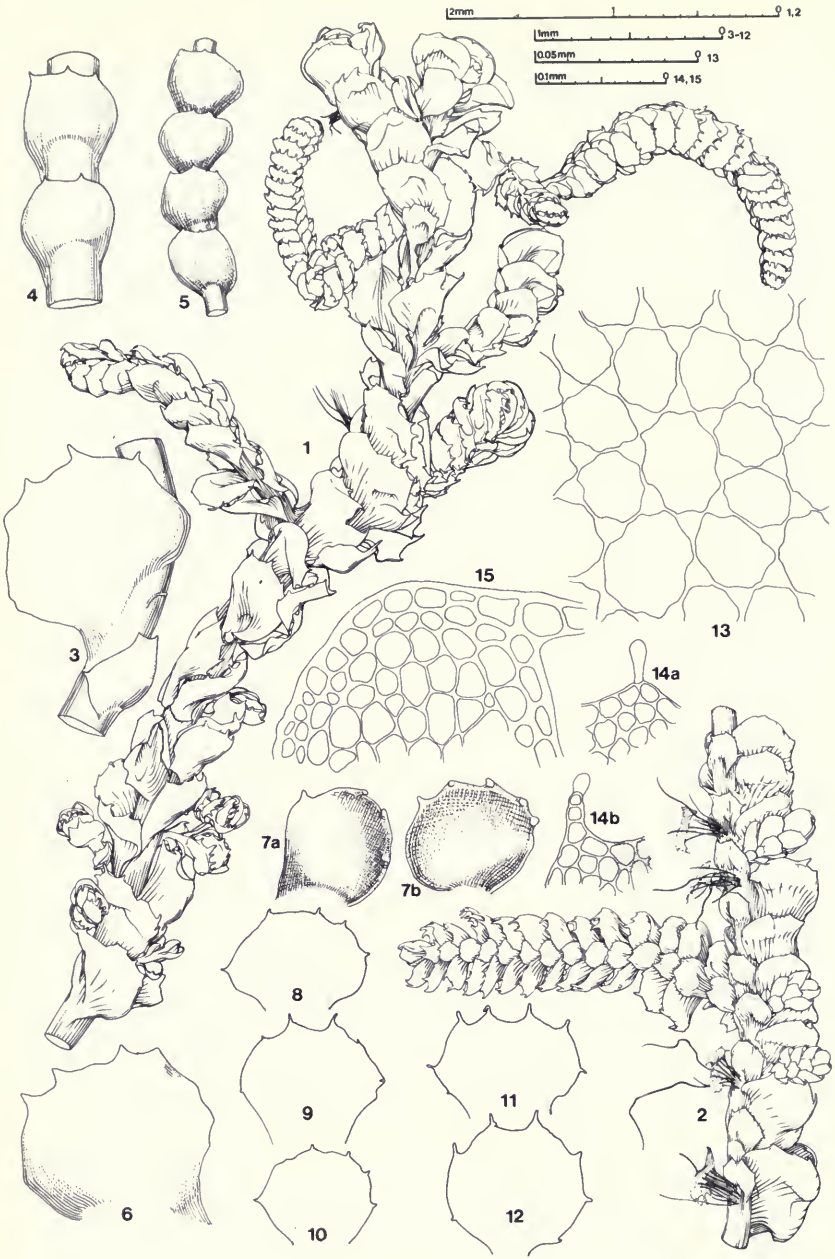
Lophocolea homomalla Steph. Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26 (III, 6):39. 1900, *syn. fide* Engel (1978). Lectotype (*fide* Engel, 1978): Chile, Prov. Aisén, R. Aisén Valley, January 1897, *Dusén 253* (S! — c. per.).

Plants prostrate, but axes often sharply curved dorsally or ventrally, often in thick, dense mats, pale green, often tinged with brown or pale brown throughout, nitid when dry; axes to 2.7 cm. tall, to 2.8 mm. wide with leaves spread.

Branches very frequent, often with copious production of short to long lateral- or ventral-intercalary branches that are narrower in width than main axis, the branches with leaves and underleaves more closely imbricate and more concave than those on main axis, giving the branches a narrow, vermiform, submoniliform appearance; ventral-intercalary branches commonly somewhat laterally displaced and those of the lateral-intercalary somewhat ventrally displaced, the ± vermiform, intercalary branches occasionally repeatedly branched and may give rise to an enlarged axis like that of the main axis, the latter of which may produce more vermiform axes; Frullania-*type branches occasional, appearing like the main axis.*

Stems 7-13 cells high, cortex in 1-2(-3 ventrally) rows of thick-walled cells the same size or slightly smaller than the medullary, the cortex commonly with 1-2 rows of dorsal cells the same size as the medullary cells and 2-3 rows of ventral cortical cells smaller than those of the medullary; cuticle smooth; endophytic hyphae absent. Rhizoids in fascicles from stem near underleaf base.

Leaves of main axis with insertion slightly recurved at ventral end; leaves loosely imbricate, adaxially concave, especially in ventral portion, wide-ovate to ± reniform; *apex broadly rounded and commonly incurved,* undivided, *usually with a few large teeth-*


2mm
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14b
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11
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12

laciniae, occasionally entire; dorsal margin straight or slightly rounded, *sinuate, occasionally ± reflexed*, short to long decurrent, entire; ventral margin broadly rounded, entire, or with a few large teeth, especially towards the apex. *Intercalary branch leaves ca. 0.5 the size of leaves, closely imbricate, more concave, more regularly toothed, the teeth sharper.*

Leaf cells thin-walled, trigones large, very often bulging, rarely confluent; median leaf cells 12-25 μ wide, (12-)17-29 μ long; cuticle smooth to roughened and appearing finely granular.

Underleaves *0.3-0.5 as long as wide, wider than stem, remote to contiguous, ± cucullate, the apical portion very frequently either approaching or in contact with stem, the basal portion abruptly convex* (ventral view); *margins curved dorsally, ± clasping stem and obliterating view of stem from lateral and ventral views; underleaves reniform to subrectangular, occasionally suborbicular; apices undivided and broadly rounded to truncate or bidentate to retuse to short-bifid*, the apices merely with 2 slime papillae or with segments or teeth terminating in a slime papilla; margins of the lamina with 1-3 slime papillae or small to large teeth each terminating in a slime papilla. *Intercalary branch underleaves more cucullate (and appearing ± inflated) and imbricate, usually undivided, less frequently retuse, rarely short-bifid.*

Plants dioecious; androecia terminal or intercalary on short or rather long lateral- or ventral-intercalary branches; bracts densely imbricate and with apices appressed to bract immediately above, the bracts strongly saccate; lobule margin with several slime papillae *and* often few-celled teeth, and a lacinium, or with 1 large, broadly rounded involute lobe; antheridia solitary, commonly orange-brown, stalk uniseriate.

Gynoecia on short, abbreviated, ventral- or lateral-intercalary branches; subfloral innovations absent; bracts in 2 series, those of innermost series subrectangular to obovate to ± spatulate; apices truncate to broadly rounded, with few to numerous teeth that often terminate in a slime papilla; margins entire. Bracteoles of innermost series free from bracts, subrectangular to obovate to ± spatulate; apices undivided and broadly rounded or retuse, with few to numerous teeth or merely with a few slime papillae; margins entire or with a few teeth or slime papillae. Perianth trigonous, elongate-subrectangular to subclavate to ± fusciform, not or barely narrowing toward the wide and open, rarely closed mouth; lobes broadly rounded, rarely incurved, but the ventral often infolded, the lobes with numerous small teeth that often terminate in a slime papilla; keel occasionally with wings of a few cells high, the wings occasionally dentate.

Seta 8-10 cells in diameter, with 26-32 rows of outer thick-walled cells (with corners thickened similar to trigones) surrounding an inner core of scattered cells that are

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Opposite:

FIG. 43. *Clasmatocolea fulvella* (Hook. f. & Tayl.) Grolle. **1,** Portion of plant, dorsal-lateral view. **2,** Portion of plant with a few branches. **3,** Portion of main axis, lateral view. **4,** Portion of main axis, ventral view. **5,** Portion of intercalary branch, ventral view. **6,** Leaf of main axis. **7.** Leaves of intercalary branch. **8-12,** Underleaves of main axis, flattened. **13,** Median leaf cells. **14,** Portions of main axis underleaf apices, each with a slime papilla. **15,** Stem of main axis, cross section. Figures 1-8, 10, 13, 14a, 15, from lectotype of *Jungermannia fulvella, Hooker*, Chile, Prov. Magallanes, I. Hermite; figures 9, 11, 14b, from *Engel 6323*, Chile, Prov. Magallanes, B. San Nicholas; figure 12, from *Engel 2998B*, Falkland Is., Mt. Adam.

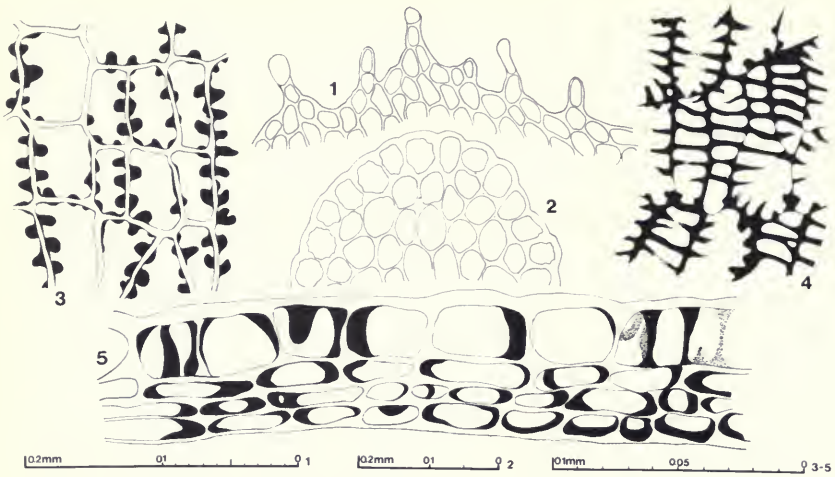


FIG. 44. *Clasmatocolea fulvella* (Hook. f. & Tayl.) Grolle. **1,** Perianth mouth. **2,** Seta, cross section. **3,** Outer capsule wall cells. **4,** Inner capsule wall cells. **5,** Capsule wall, cross section. Figure 1, from *Engel 3006*, Falkland Is., Mt. Adam; figures 2-5, from *Engel 6125*, Chile, Prov. Magallanes, B. Borja.

smaller, equal to, or slightly larger than the outer row. Capsule broadly ovate to elliptic, the valves 0.91-1.19 mm. long, 41-53 μ thick, of 4-5 layers, rarely (and very locally) in 3 layers, the outer row of cells equal to thickness of 2.5-3 of interior strata; outer layer with red-brown, nodule-like to ± spinelike thickenings that are often feebly tangentially dilated, a very few semiannular bands occasionally present; exposed wall thickened; intermediate and inner layers of cells subequal in thickness, the intermediate layers with thickenings occasionally feebly extending onto tangential walls; inner layer of cells with red-brown semiannular bands, the bands often incomplete, the radial walls with nodulose thickenings often present.

Spores 13-17 μ, light brown, exine with the light microscope appearing minutely punctate, but under the SEM with rather densely granulate to short vermiform projections covered with often crowded nanogranules, the intervening hollows with isolated nanogranules; spores averaging 1.9 × elater diameter. Elaters 7-9 μ wide, tapering gradually toward ends, apical portion often with thick, nonspiral walls, elater walls light brown.

Clasmatocolea fulvella forms a transition of sorts between Sect. *Clasmatocolea*, to which it is allied, and Sect. *Puccioanae* (Subg. *Metaclasmatocolea*). *Clasmatocolea fulvella* is allied to Sect. *Puccioanae* because it shares, with *C. puccioana*, a highly unique branching pattern within the genus. The branches in these two taxa are copiously produced, with the intercalary branches vermiform and submoniliform, narrow, smaller in width than main axis, and usually short and abbreviated.

Variation.—The variability in position of ventral- and lateral-intercalary

branches in *C. fulvella* is worthy of note. In this species ventral merophytes are very wide, which allows for branch development from the lateral portions as well as from the middle of the merophyte. This condition, which also occurs in the genus *Calypogeia*, explains the lateral displacement of ventral-intercalary branches in *C. fulvella* (B. Stotler, *in litt.*). The lateral-intercalary branches commonly are somewhat ventrally displaced and occur close to the ventral merophyte in the following positions: (a) very close to the ventral base of the leaves and not in close proximity with an underleaf; (b) at the very edge of the underleaf; or (c) between the underleaf and the ventral insertion of the leaf.

Differentiation.—Clasmatocolea fulvella is a distinctive taxon and should not be confused with any other member of the genus.

The underleaves show little variability and possess characteristics very distinctive of the species. The main axis underleaves are reniform to suborbicular to subrectangular in outline, have apices very frequently either approaching or in contact with the stem, and become abruptly convex (ventral view) near the insertion. The margins are curved dorsally, ± clasping the stem and obliterating a view of the stem from lateral and ventral views, lending the underleaf a cup-shaped appearance. The underleaf apices are broadly rounded to truncate at the apex, which is bidentate to retuse.

The branching is also distinctive for the species. The intercalary branches are often copiously produced and are narrowly vermiform, ± submoniliform, and considerably narrower than the main axis. Compared to the main axis, the intercalary branch *leaves* are ca. 0.5 the leaf size, more closely imbricate, more concave, more regularly and sharply toothed, less sinuate, and with apices less incurved, whereas the intercalary branch *underleaves* are considerably smaller, more closely imbricate, more cupulate (appearing ± inflated), and have apices less frequently retuse and only rarely short-bifid.

The lateral-intercalary branches of *C. fulvella* are usually present, but if absent, this species may be confused with *C. humilis*. *Clasmatocolea fulvella*, when moistened, has main axis leaves sinuate and incurved and has main axis underleaves ± clasping the stem, never spreading and with apices very frequently either approaching or in contact with the stem. *Clasmatocolea humilis*, on the other hand, when moistened, has main axis leaves plane and has main axis underleaves not clasping the stem, occasionally spreading and with apices not lying in contact with the stem. The dentate to laciniate leaves of *C. fulvella* may be used as a supplementary character to separate the species from *C. humilis* var. *humilis*.

Another condition, the reverse of the above, occasionally occurs—the

plants superficially appear to consist mainly of masses of branches, with the distinctive combination of main axis and branches not apparent. In this case the main axes should be searched for carefully. In the median portion of a colony the main axes often are hidden and in various stages of decay, likely resulting from the more vigorous growth of the younger branches. The marginal portions of colonies exhibit well-developed, vigorous main axes more typical of the species. In either instance, the very distinctive characters of the branch leaves and underleaves discussed above should be utilized to identify the species. This condition occurs particularly where the species grows closely appressed to bark.

Clasmatocolea fulvella may be confused with some phenotypes of *C. humilis* var. *suspecta;* see under the latter for comments to distinguish these taxa.

Notes.—1. In their original description of *Jungermannia fulvella*, Hooker & Taylor (1844) make no mention of a perianth or sporophyte, but three years later (Taylor & Hooker, 1847), they describe a perianth and include a figure of a sporophyte-bearing plant in their plate of the species. Taylor & Hooker (1847) are thus typifying the species as possessing both perianths and sporophytes; I have designated as a lectotype a specimen in the *Taylor Herbarium* (FH) that has both these structures represented.

2. There are two taxa that comprise the syntypes of *Lophocolea homomalla—C. cucullistipula* and *C. fulvella*. Stephani (1900, p. 40) states for the Río Aisén material, "in ramulis et truncis putridis." The material collected "in ramulis" is *C. cucullistipula*, whereas that on "truncis putridis" is *C. fulvella*. The protologue resembles the *C. fulvella* material more closely, particularly with regard to the comment on branching and the description of the underleaves. Because perianths are described in the original description, the lectotype must contain perianth-bearing plants. Stephani in his *Species Hepaticarum* (1906, p. 78) states, "typhus in herb. Stephani," so, with this in mind, I searched for perianths among the Geneva material, but was unsuccessful. I therefore excluded Stephani Herbarium material from consideration of a lectotype. I have studied Dusén collected material of *L. homomalla* from a number of herbaria, but have not seen specimens from Isla Guaitecas, Boca Chica, the second of two localities mentioned by Stephani. Three of the four collections from G were labeled merely "Patagonia," without a specific locality, and it is quite possible that at least some of these were gathered at Boca Chica.

The Stephani Icones of *L. homomalla* (*Icones Hepaticarum, Lophocolea* No. 90) is a mixture of information relating to both *C. fulvella* and *C. cucullistipula*. The figure of a stem with an attached underleaf and pair of leaves is of *C. fulvella*, yet within the leaf there is a note that the trigones

FIG. 45. *Clasmatocolea fulvella* (Hook. f. & Tayl.) Grolle.

are "magn. contig.," a feature more relevant to *C. cucullistipula.* The figures of bracts, bracteole, and perianth mouth are much closer to *C. cucullistipula.*

Ecology.—In the Magellanian region, very sporadic on rotted wood in well-shaded forests (sea level) or over rock in more open subalpine areas. In the Valdivian region the species seems more altitudinally zoned, occurring 900-1,700 m. in forests. Here the species grows nearly exclusively on rotted, decorticated wood in forests of the following types: *Nothofagus pumilio*, *Nothofagus* scrub, *Fitzroya*, *Araucaria*, and *Araucaria-Nothofagus pumilio* (in the latter two forest types the species is one of a few hepatics growing on rotted, decorticated *Araucaria* wood, where it is quite common).

Phytogeography.—Falkland Is. (320-700 m.); rather common in Tierra del Fuego (300-600 m.); N. to 36° 50′ S. in West Patagonia; also in Parque Nac. Nahuel Huapí of Andean Patagonia (see fig. 45).

Specimens seen.—**FALKLAND IS.** (selected). **EAST FALKLANDS:** Stanley Region, summit of Mt. Kent, 455 m., *Engel 2753*, *2759* (MSC). **WEST FALKLANDS:** Port Howard, Freezer Rocks, on E. slope of Mt. Maria, 320 m., *Engel 3143*, *3150* (MSC); Mt. Adam, *Halle & Skottsberg 226* as *L. puccioana* (UPS); Weddell I., *Halle & Skottsberg 226* as *L. puccioana* (UPS). **ARGENTINA.** TERR. TIERRA DEL FUEGO: I. des los Estados, *Spegazzini 63*[4] (VER); ibid., Pto. Cook, *Skottsberg s.n.* (S); ibid., *Skottsberg s.n.* as *L. gayana* (S); ibid., M. Conegliano, *Spegazzini 8* as *L. puccioana* (NY); I. de los Estados, Pto. San Juan del Salvamiento, *Spegazzini 51* (NY, VER — c. per.); Carbajal Valley, base of Sa. de Sorondo, 300 m., *Crow 1784* — c. sporo., *1797* — c. sporo. (MSC); C. Garibaldi, SE of L. Escondido, near Rte. 3 from Ushuaia to R. Grande, 600 m., *Schuster 58312a* (hb. Schuster); Paso Garibaldi, 460-470 m., *Roivainen 579*, *580* — c. per. (F, H); Sa. Alvear, 370 m., *Roivainen 846* — c. sporo. (F, H). **CHILE.** PROV. MAGALLANES: "S. part of Tierra del Fuego," *Darwin 467* (FH — c. sporo., NY); Cabo de Hornos, *Antarc. Exped.* as syntype of *J. fulvella* (NY); ibid., *Davis s.n.* (FH, S); ibid., *Hooker s.n.* as syntype of *J. fulvella* (NY); I. Hermite, *Hooker s.n.* as syntype of *J. fulvella* (NY, S); ibid., *sin. coll.* as *L. cookiana* (PC); B. Orange, *sin. coll. 104* (PC); R. Azopardo, *Dusén 51* as *L. humilis* (LD — c. per., UPS); ibid., *Dusén 86* (NY, S); Cta. Gomez, *Halle & Skottsberg 207* as *L. homomalla* (S); I. Desolación, *Dusén* (NY, S); ibid., Pto. Angosto, *Dusén s.n.* as *L. humilis* (S); ibid., *Dusén 180* as *L. humilis* (UPS); ibid., *Dusén 263* (S); Brunswick Pen. (cf. Engel, 1978); E. side of B. Borja, *Engel 6125*, *6232A* (MSC); Can. Gajardo, Cta. Inga, *Halle & Skottsberg 202* — c. per. + ♂ (S); B. Sholl, *Discovery Exped. 982/I* (hb. Grolle); head of F. Peel, *Engel 5502* — c. sporo. (MSC).

PROV. AISÉN: R. Aisén, *Dusén s.n.* as syntype of *L. homomalla* (NY, S); ibid., *Dusén 253* as syntype of *L. homomalla* (S); ibid., *Dusén 263* (NY); ibid., *Dusén 287* as syntype of *L. homomalla* (FH); Pto. Puyuhuapi, 1,700 m., *Schwabe 32 ex p.* (JE); C. Tesoro, 1,000 m., *Schwabe 39/c* as *L. homomalla* (JE); ibid., 900 m., *Schwabe 40a* (hb. Grolle — c. per. + ♂, JE). PROV. CHILOÉ: Pto. Quellon, *Halle & Skottsberg 220* as *L. navistipula* (UPS). PROV. OSORNO: Antillanca, 1,180 m., *Ruthsatz 54/17* (JE); Refugio Antillanca, 1,160 m., *Engel 3915B* (F); 0.5 km. by road below Refugio Antillanca, 1,000 m., *Engel 11504* (F). PROV. VALDIVIA: Cord. Pelada, summit of El Mirador, between La Union and Pta. Hueicolla, 1,000 m., *Engel 12391* (F); V. Shoshuenco, *Ruthsatz 49/16*, *49/49* (hb. Grolle); SW slope of V. Quetrupillán, 1,160-1,450 m., *Engel 11159* — c. sporo., *11162* — c. sporo., *11164* (F). PROV. CAUTÍN: V. Lanín, 1,220 m., *Ruthsatz s.n.* (JE); L. Quilleihue, 10.7 km. by road E. of Puesco, ca. 7 km. by road W. of Chile-Argentina boundary, 1,050 m., *Engel 11311* (F); V. Llaima, 1,260-1,280 m., *Ruthsatz s.n.* (JE); Parque Nac. Conguillo, 1,140-1,150 m., *Mahu 10787*, *10796*, *10835* (hb. Mahu). PROV. MALLECO: Parque Nac. Nahuelbuta, Pino Hueco, 1,400 m., *Mahu 6055* (hb. Grolle, JE, hb. Mahu). PROV. MALLECO/PROV. ARAUCO: Cord. Nahuelbuta, Parque Nac. Nahuelbuta, W. of Angol, 1,280-1,300 m., *Engel 12594*, *12603* — c. sporo., *12627* (F). PROV. CONCEPCIÓN: Concepción, *Dusén s.n.* as *L. humilis* (S); ibid., *Dusén 180* as *L. humilis* (NY). **ARGENTINA.** PROV. NEUQUÉN/PROV. RÍO NEGRO: Parque Nac. Nahuel Huapí, *Donat 27 ex p.* as *L. homomalla* (S); ibid., 800 m., *Donat 61 ex p.* (JE); L. Nahuel Huapí, Puerto Blest, *Donat 136/a* (JE).

Sect. **STRONGYLOPHYLLAE** Engel, sect. nov.

Foliorum caulinarum cuticula habens grossas hemisphaericas hyalinas papillas.

Type species: *Clasmatocolea strongylophylla* (Hook. f. & Tayl.) Grolle.

Leaf cuticle with coarse, hemispherical, hyaline papillae.

Distribution.—New Zealand and its subantarctic islands, Tasmania, Java.

Clasmatocolea strongylophylla (Hook. f. & Tayl.) Grolle. Figures 46,47, Plates 21,22.

Jungermannia strongylophylla Hook. f. & Tayl. London J. Bot. 3:370. 1844. *Alicularia strongylophylla* (Hook. f. & Tayl.) G. L. & N. Syn. Hep. 619. 1846. *Leptoscyphus strongylophyllus* (Hook. f. & Tayl.) Mitt. Hooker's J. Bot. Kew Gard. Misc. 3:358. 1851. *Leioscyphus strongylophyllus* (Hook. f. & Tayl.) Mitt. *in* Hooker, Bot. Antarc. Voy. 3:225. 1859. *Mesophylla strongylophylla* (Hook. f. & Tayl.)

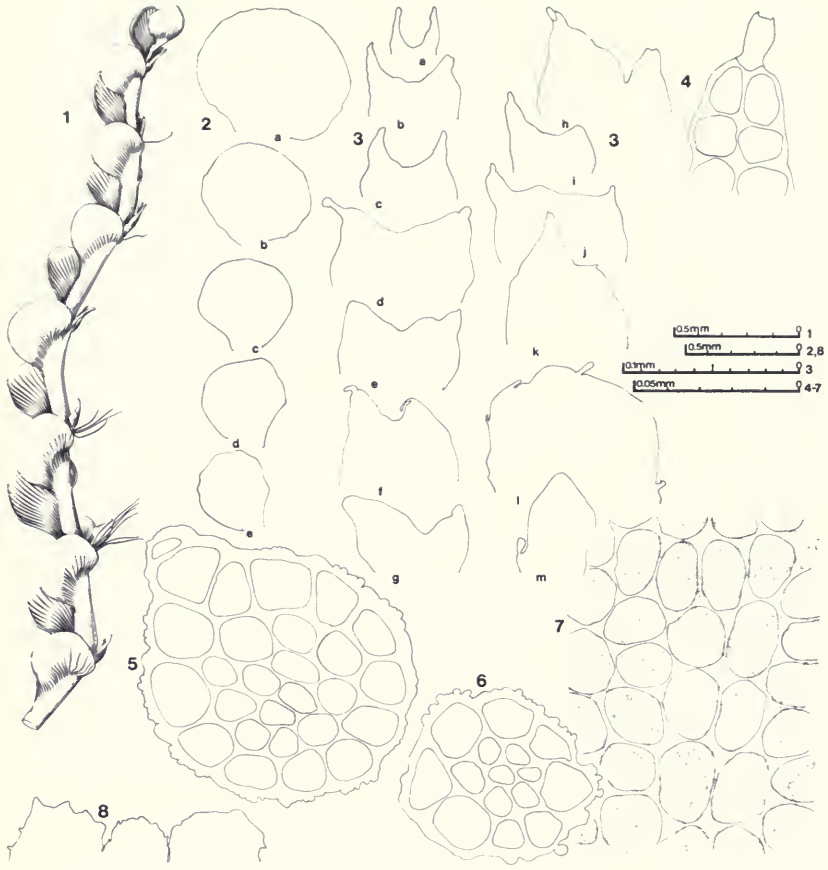


FIG. 46. *Clasmatocolea strongylophylla* (Hook. f. & Tayl.) Grolle. **1,** Portion of main axis, dorsal view. **2a-e,** Leaves. **3a-m,** Underleaves. **4,** Underleaf segment, apical portion with partially collapsed slime papilla. **5-6,** Stem, cross sections. **7,** Median leaf cells showing coarsely papillose cuticle. **8,** Perianth lobes, ventral lobe in middle. Figures 1, 2c, d, 3b, i, m, 4, 5, 7, from type of *C. strongylophylla*, *Hooker*, Campbell I. (S); figure 2a, from *Langridge 179*, New Zealand, Harihari; figures 2b, 3e, j, b, from *G. Scott*, New Zealand, S. of Dunedin; figures 2e, 3g, from *Hooker*, Auckland Is.; figure 3a, from type of *C. strongylophylla* var. *β minor*, *Hooker*, Auckland Is.; figure 3c, from *D. Scott 208*, New Zealand, Godley R. Valley; figure 3d, from *Wilson 2775*, New Zealand, Mt. Cook Natl. Park; figures 3f, k, l, from type of *J. turgescens*, *Hooker*, Auckland Is.; figures 3h, 8, from *Schuster 48481*, New Zealand, Otira R. Gorge.

Trev. Mem. Ist. Lomb. Sci. Lett. III. 4:398. 1877. *Lophocolea strongylophylla* (Hook. f. & Tayl.) Hodgs. Trans. Roy. Soc. New Zealand 80:338. 1953. *Clasmatocolea strongylophylla* (Hook. f. & Tayl.) Grolle, Rev. Bryol. Lichénol. 29:73. 1960. Original material: Campbell I., *Hooker* (BM!, S! — c. ♂ + young per.).

Jungermannia strongylophylla var. *β minor* Hook. f. & Tayl. London J. Bot. 3:370. 1844, *syn. fide* Grolle (1962). *Alicularia strongylophylla* var. *minor* (Hook. f. & Tayl.) G. L. & N. Syn. Hep. 619. 1846. Original material: Auckland Is., *Hooker* (BM!, L!).

Jungermannia turgescens Hook. f. & Tayl. London J. Bot. 3:375. 1844, *syn. fide* Grolle (1962). *Leptoscyphus turgescens* (Hook. f. & Tayl.) Mitt. Hooker's J. Bot. Kew Gard. Misc. 3:358. 1851. *Leioscyphus turgescens* (Hook. f. & Tayl.) Mitt. *in* Hooker, Bot. Antarc. Voy. 3:225. 1859. *Mylia turgescens* (Hook. f. & Tayl.) Trev. Mem. Ist. Lomb. Sci. Lett. III. 4:412. 1877. *Lophocolea turgescens* (Hook. f. & Tayl.) Hodgs. *in* Martin, Trans. & Proc. Roy. Soc. New Zealand 78:495. 1950. *Clasmatocolea turgescens* (Hook. f. & Tayl.) Grolle, Rev. Bryol. Lichénol. 29:73. 1960. Original material: Auckland Is., *Hooker* (LD! — c. per., S! — c. per.).

Lophocolea angulistipula Steph. Bull. Herb. Boissier 6 (9):791. 1906 (= Spec. Hep. 3:91), *syn. nov. Clasmatocolea angulistipula* (Steph.) Grolle, Rev. Bryol. Lichénol. 29:71. 1960. Holotype: Tasmania, Mt. Wellington, St. Crispin's, 24 January 1899, *Weymouth 1514* (G!).

Plants rather delicate, prostrate, usually creeping among other bryophytes, occasionally caespitose, green to light or dull brown; *axes 250-950 μ wide* without leaves spread.

Branching sparing, *mostly of* Frullania-*type*, *occasionally of ventral-intercalary type*, *lateral-intercalary type very rare*.

Stems *4-7 cells high*, *cortex in a single layer of thick-walled cells usually moderately to considerably larger* than but occasionally ca. same size as medullary cells; *cuticle with low*, *rounded to hemispherical papillae* or rarely striate; endophytic hyphae rare. Rhizoids in fascicles from stem at base of underleaves.

Leaves with insertion narrow, slightly to distinctly recurved at ventral end; *leaves erect to slightly spreading*, *distant* (especially in smaller plants) *to loosely imbricate*, strongly adaxially concave, *orbicular to reniform* (-obovate); apex broadly rounded to truncate to subretuse, undivided, often incurved, *the apices and margins entire;* dorsal margin long decurrent.

Leaf cells *thin to slightly thick walled*, *trigones large to bulging*, occasionally confluent; median leaf cells 10-20(-24) μ wide, 12-23(-28) μ long; *cuticle*, including that of leaf margin, *with coarse*, *hemispherical-oblong*, *hyaline*, *usually juxtaposed papillae*, very rarely wide-striate, *cuticle of basal cells often wide-striate*.

Underleaves *1 to slightly over 2* × *stem width*, transversely or obliquely inserted, free or weakly connate on 1 side, slightly to (often) strongly spreading, usually plane,

sometimes weakly convex (ventral view); underleaves *polymorphous, often with lobes of different size and configuration*, occasionally undivided and then lanceolate or oblong to ± orbicular to cuneate with usually a truncate apex, *bifid to 0.5;* segments, when present, directed laterally or toward stem apex, medium-triangular to lanceolate or reduced to a rounded projection, tooth or slime papilla, or the segments often apiculate and terminating in a slime papilla, the segment margins entire; sinus broadly rounded to often lunate; *margins of the lamina entire or with 1-2 slime papillae*, very rarely with a small tooth terminating in a slime papilla.

Plants dioecious; androecia intercalary on main axis or *Frullania*-type branches, the entire bract strongly saccate, and with apices sometimes appressed to bract immediately above; lobule margin slightly incurved, broadly rounded, entire or with 1 slime papilla; antheridia solitary, stalk uniseriate.

Gynoecia on main axis, long ventral-intercalary branches or subfloral innovations; subfloral innovations usually from below innermost bracteole; bracts in (2-)3 series, those of innermost series with apices often more incurved than in leaves, the apices and margins entire. Bracteoles of innermost series free from bracts, oblong to obovate to subsquarrose; apices emarginate or to 0.2-bifid; lamina margins with several slime papillae; bracteoles occasionally not or hardly larger than the underleaves, and then bracteoles undivided and elliptical. *Perianth somewhat inflated, terete to obscurely trigonous to bilaterally compressed, ± clavate, expanding toward mouth, the mouth somewhat to distinctly closed by incurved lobes;* dorsal lobes broadly rounded, occasionally emarginate, with a few slime papillae and rounded teeth of varying sizes, occasionally entire; *ventral lobe smaller* and often more narrowly rounded, variable in size, slightly convex, to concave, to folded inward, the latter thus giving the perianth a bilaterally compressed appearance, the ventral lobe sometimes retuse, with a few slime papillae and a tooth or entire; keels (especially the ventral) winged.

Seta not seen. Capsule wall 36 μ thick, of 4 layers, outer row of cells equal to thickness of 2 of intermediate strata; outer layer with red-brown thickenings, the thickenings of blunt-tipped spines, semiannular bands common, complete or incomplete, somewhat thickened, the thickenings occasionally nodule-like; exposed wall thin; inner layer of cells with yellow or red-brown nodule-like or spinelike thickenings, semiannular bands often present.

Spores 11-12 μ, light brown, exine with the light microscope appearing minutely punctate-short vermiculate, but under the SEM with a network of very wide, irregular, often coalescing vermiform ridges covered with nanogranules; spores *averaging 1.2 × elater diameter*. Elaters 9-11 μ wide, tapering slightly toward tips, apical portions often with thick, nonspiral walls, elater walls red-brown.

Variation.—The perianths of *C. strongylophylla* vary from terete to obscurely trigonous to bilaterally compressed. The ventral lobe is consistently smaller (often strikingly so) than the dorsal pair and varies from slightly convex to concave to distinctly infolded. In the latter instance the perianths appear bilaterally compressed. This kind of variation is not unusual within a single species in the Lophocoleaceae, i.e., in the genus *Leptoscyphus*, which nearly always has strongly bilaterally compressed perianths, a ventral lobe is commonly present that varies in stature and is particularly well developed in some specimens of, for example, *L. expansus* and *L. horizontalis*.

Differentiation.—The polymorphic underleaves of *C. strongylophylla* are diagnostic, especially with regard to the lobes, which vary in configuration, length, and overall stature, usually with one lobe of a different size and configuration than the other. On a given axis there are commonly bifid or bidentate underleaves among those that are undivided and lanceolate, with one lobe reduced to a tooth or slime papilla. Underleaves of variable sizes and configurations can usually be demonstrated on a single axis. The polymorphous underleaves, coupled with the coarse, hemispherical, hyaline, juxtaposed cuticular papillae, the large to bulging trigones, the small axis size (250-950 μ wide), and the perianths with a smaller ventral lobe that is commonly slightly to distinctly infolded, will serve to separate this species from all others of the genus.

Notes.—1. The original material of *Jungermannia strongylophylla* deposited in the British Museum is somewhat flaccid and has rather poorly developed cuticular papillae, whereas original material of the species deposited in Stockholm (S) is not flaccid and has well-developed cuticular papillae.

Original material of *J. strongylophylla* consists of brownish, very small plants with distant to contiguous leaves that have a loose network of cells with cuticular papillae ± hemispherical and rather closely juxtaposed. On the other hand, original material of *J. turgescens* consists of light brown, quite robust plants (0.63-0.95 μ wide) with loosely imbricate leaves that have a dense network of cells, with the cuticle possessing at most scattered, ± hemispherical papillae or wide striae.[8] Portions of leaves of the latter may even have a smooth cuticle. I can, however, find no consistent character to separate *C. turgescens* from *C. strongylophylla*, and I therefore regard the original material of *Jungermannia turgescens* as an extreme in a continuum with *C. strongylophylla* and concur with Grolle (1962) in treating them as conspecific.

2. Stephani (1906) used the spelling *Lophocolea angulistipula*, although the name written on the label of the type specimen is *Lophocolea angulistipa*. This is a case of Stephani changing his mind regarding the spelling of a name to be published (cf. Engel, 1973b).

3. Reports of this species (sub *Leioscyphus turgescens*) from southern South America and Kerguelen are erroneous. Those from Isla Desolación are *C. gayana*, whereas those from Kerguelen are *C. humilis*. Although I have not seen Río Azopardo collections, I would not expect the species to occur there.

[8] The large cuticular papillae are sometimes (as in original material of *J. turgescens*) nearly transparent and thus difficult to demonstrate and must be searched for with care.

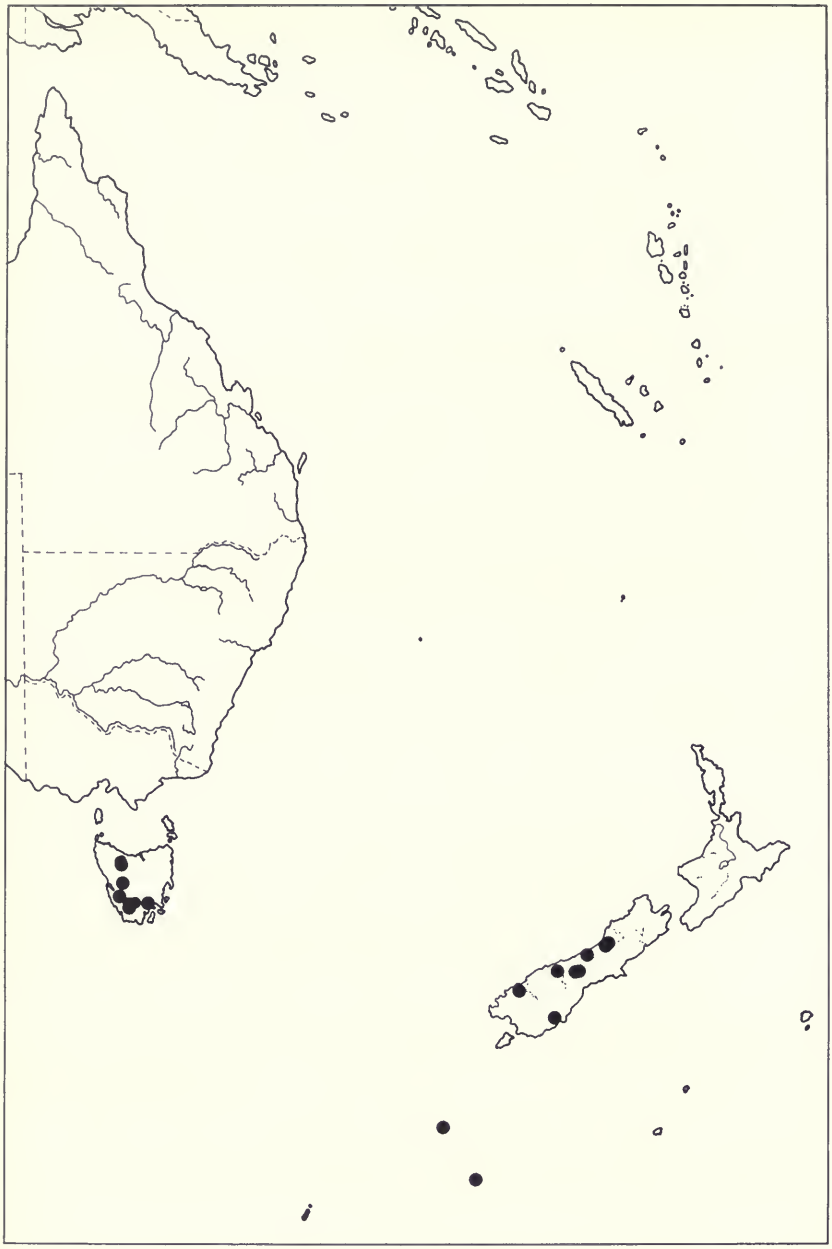


FIG. 47. *Clasmatocolea strongylophylla* (Hook. f. & Tayl.) Grolle.

Ecology.—In New Zealand on steep, shaded, humid, or dripping cliffs or rock faces in *Nothofagus menziesii* forests (with *Blepharidophyllum vertebrale* and *Lepidozia spinosissima*, etc.) or tall subalpine scrub. Sometimes on wet, rocky, or sandy banks by roadsides where occasionally with *Bryum laevigatum*. In Tasmania mostly above 900 m. and in subalpine situations. It grows on soil over boulders or under protective cover of scrubby vegetation, either on soil or on dripping cliff faces. Also in *Nothofagus gunnii-Eucalyptus coccifera* forests where again it is associated with more moist microhabitats, such as boulders of stream banks or lake shores.

Phytogeography.—Campbell I.; Auckland Is.; New Zealand, South I. (90-1,370 m.); Tasmania (sea level-1,310 m.) (see fig. 47).

Specimens seen.—**CAMPBELL I.:** Mt. Beeman, *Members of 1958 Expedition s.n.* as *C. turgescens* (CHR). **AUCKLAND IS.:** *Sin. coll.* — c. ♂ (BM); *Erebus & Terror Exped.* — c. per. (BM); *Hooker s.n.* (BM, L, NY); Hooker Hills, *Fineran s.n.* (hb. Grolle). **NEW ZEALAND. SOUTH ISLAND.** OTAGO: Waipori Road, S. of Dunedin, ca. 300 m., *Scott s.n.* — c. per. (CHR); Waipori Road, W. of Dunedin, 490 m., *Scott 15* (hb. Monash Univ.). Fiordland Natl. Park, track from L. Mackenzie to Harris Saddle, Humboldt Mts., *Schuster 67-504* (F, hb. Schuster); Fiordland Natl. Park, Humboldt Mts., N. of Earland Falls, on track to L. Mackenzie, *Schuster 67-3456B* (F, hb. Schuster); Fiordland Natl. Park, L. Mackenzie to Harris Saddle, above Hollyford Valley, Route Burn Track, 90-155 m., *Schuster 67-3904* (F, hb. Schuster). SOUTHLAND: "Head of Hollyford R., Doubtful Sound area," *Martin s.n.* (hb. Grolle). WESTLAND: Pleasant Flat on Haast Pass Road, *Allison s.n.* (CHR); 0.6 mi. N. of Haast Pass, 520 m., *Schuster 53380a* as *C. turgescens* — c. per. + ♂ (hb. Schuster); Harihari, *Langridge 179* as *C. turgescens* (CHR); Arthur's Pass Natl. Park, Otira R. Gorge, W. of Arthur's Pass, ca. 300-365 m., *Schuster 48481* as *C. turgescens* — c. sporo. + ♂ (hb. Grolle, hb. Schuster, TNS); ibid., *Schuster 48484b* as *C. turgescens* — c. ♂ (hb. Schuster); Otira Pass, *?Jack s.n.* as *C. turgescens* (CHR). CANTERBURY: Mt. Cook Natl. Park, edge of Governors Bush, ca. 720 m., *Wilson 2775* (CHR); mid Godley R. Valley, 1,370 m., *D. Scott 208* (CHR). **TASMANIA:** Kermandie R. at North Cr., ca. 50 m., *Norris 29394* (F); Mt. Field Natl. Park, *A. Ratkowsky 78/171* (F); ibid., Beatties Tarn, 975 m., *Engel 14509A* (F); Mt. Field Natl. Park, just below SE end of L. Fenton, Lady Barron Cr., 1,000 m., *Engel 13067* — c. per., *13075A* (F); Mt. Field Natl. Park, just S. of L. Fenton and NE of Wombat Moor, 1,020 m., *Engel 13268* (F); Mt. Field Natl. Park, Mt. Mawson Plateau, 1,200 m., *A. Ratkowsky 78/75* (F); ibid., above and W. of L. Dobson and S. of L.

Seal, 1,250 m., *Engel 13091* — c. sporo. (F); Mt. Field Natl. Park, Tarn Shelf, below and E. of Rodway Range, 1,270 m., *Engel 14355*, *14368* (F); Mt. Field Natl. Park, Rodway Range, between Rodway Ski Tow and K Col area, 1,240-1,310 m., *Engel 14393* (F); Mt. Field Natl. Park, L. Belcher, ca. 900 m., *Norris 28619*, *28621* (F); plateau region E. and SE of Mt. Eliza summit, E. of L. Pedder, ca. 1,225 m., *Engel 13713* — c. ♂ (F); Mt. Sprent, *A. Ratkowsky 78/172* (F); Gordon R. just E. of confluence with Serpentine R., WNW of Strathgordon, 350 m., *Engel 13831* — c. ♂, *13841* (F); Gordon R., Sir John Falls, just up river from Butler I., sea level, *Engel 14683* — c. sporo. (F); Mt. Rufus, *A. Ratkowsky 79/15* (F); Mt. King William I, 1,200 m., *A. Ratkowsky 77/76* (F); E. slope of Black Bluff just below summit, S. of Burnie, 1,250 m., *Engel 15800*, *15807A* — c. per. (F); SW slope of St. Valentines P., SSW of Burnie, 920-1,100 m., *Engel 15633* — c. per. (F).

Clasmatocolea tjiwideiensis (Sande-Lac.) Grolle. Figure 48.

Chiloscyphus tjiwideiensis Sande-Lac. Ned. Kruidk. Arch. 3:418. 1854. *Anthoscyphus tjiwideiensis* (Sande-Lac.) Trev. Mem. Ist. Lomb. Sci. Lett. III. 4:422. 1877. *Conoscyphus tjiwideiensis* (Sande-Lac.) Schiffn. Consp. Hep. Arch. Ind. p. 124. 1898. *Clasmatocolea tjiwideiensis* (Sande-Lac.) Grolle, Rev. Bryol. Lichénol. 29:73. 1960. Original material: Java, Crater Tjiwidei, *Junghuhn* (L no. 910. 288-134!).

Plants *soft*, *spongy*, *delicate*, apparently prostrate, yellow-brown or light brown; *axes 0.65-0.91 mm. wide.*

Branches occasional, *of ventral-intercalary type.*

Stems rather slender for plant size, *flexuous*, sometimes golden brown, *6-9 cells high*, *the cortex hardly differentiated*, in 1-2 rows of moderately to distinctly thick-walled cells ± same size as medullary cells; cuticle papillose; medullary cell walls moderately to distinctly thickened, the thickenings of ± same magnitude as those of cortical cells; endophytic hyphae in both cortical and medullary cells. *Rhizoids magenta*, in dense fascicles from stem very near underleaf base, occasionally from stem near ventral base of leaf.

Leaves with insertion sharply recurved at ventral end; *leaves strongly erect*, *dorsally connivent*, rather loosely imbricate, distinctly conchiform concave, *oblate to subsquarrose;* apex broadly rounded, undivided, *entire*, sometimes repand; dorsal margin ± straight (at least in proximal ca. 0.75), often moderately wavy, often slightly recurved, *entire or with 1-2 sharp*, *often hooklike teeth* in median and/or lower portion, the *margin conspicuously long decurrent;* ventral margin very broadly rounded, the *basal portion nearly always with 1-2(-3) few-celled*, *sharp or blunt teeth*, *the armature on that portion of margin decending below stem*, the margin decurrent, *sometimes strongly so and then connate with basal*, *adaxial surface of underleaf.*

Leaf cells thin to moderately thick-walled, the trigones medium to large, the sides straight to slightly bulging, with secondary cell wall thickenings occasional; median leaf cells (25-)28-37 μ wide, 28-38(-42) μ long, *cuticle*, including that of leaf margin,

with hemispherical-oblong, hyaline, usually juxtaposed papillae, the cuticle of basal cells papillose-striate to striate.

Underleaves 3.3-4 × stem width (when underleaf flattened), *connate on 1 or both sides with ventral-basal, adaxial portion of leaf lamina;* underleaves narrow, slightly spreading, distant to approximate, *deeply convex to ± cupulate* (ventral view), ovate to suborbicular; *apices variable* (usually so on same axis): undivided and 1- or bidentate or divided to 0.45; segments, when present, somewhat incurved, the segment margins entire; *margins of the lamina 1-3-dentate, rarely entire*, short to long decurrent.

Plants apparently dioecious; androecia not seen. Gynoecia on leading axes, only immature individuals seen.

Differentiation.—The following combination of features will distinguish this species from all others in the genus: (a) the coarse, hemispherical, hyaline papillae of the leaves; (b) the strongly erect, dorsally connivent, oblate to subsquarrose leaves with dorsal margin straight (at least for the most part), and conspicuously long decurrent on the stem; (c) the 1-3 few-celled teeth on the basal portion of the ventral margin (and usually situated on that portion of the margin extending ventrally beyond the stem); (d) the relatively small stems that are 6-8 cells high and possess very thick-walled cells, with very little, if any, cortical differentiation; (e) the magenta-colored rhizoids (unique to genus); (f) the relatively large underleaves that are rather deeply convex (ventral view) to ± cupulate and (when flattened) ca. 3.3-4 × the stem width.

This species appears to be related to *C. strongylophylla* of New Zealand and Tasmania, which also has (a) coarse, hemispherical papillae on the leaves; (b) long decurrent dorsal margins of leaves; (c) thick-walled stem cells that are of a comparatively few number of cells high; and (d) polymorphous underleaf apices—either undivided or distinctly bifid. *Clasmatocolea tjiwideiensis* may be distinguished from *C. strongylophylla* by (a) the connate underleaves; (b) the leaf armature; (c) the underleaves that are deeply convex (ventral view) to ± cupulate and wider, being ca. 3.3-4 × the stem width; and (d) the larger median leaf cells.

Notes.—1. The underleaves are connate on one or both sides with the ventral-basal, adaxial surface of the leaf lamina. This feature is often a subtle one, and to observe it, an axis should be examined in both ventral and dorsal views while slowly and carefully rotating the axis. When connate on both sides, the attachment on one side is usually more obvious than on the other, depending on distance of the attached leaf. For this reason, where leaves are more distant on an axis, the attachment on one side disappears, and here the underleaves are connate on only one side; the character should be studied on well-developed portions of the axis with leaves more closely imbricate.

2. This species has not been collected since the mid-nineteenth century.

1mm
1-3
1
2
3
4
1mm
4
5
6
7
8
9
10
11
12
13
14
1mm
0.5
5-9
0.1mm
0.05
10
0.2mm
0.1
11-14

Ecology-Phytogeography.—Endemic to Java, where at least sometimes corticolous; altitudes of ca. 1,830 m. are recorded.

Specimens seen.—**JAVA:** Mt. Salak, 1,830 m., *Kurz s.n.*, *177* (L).

Subg. **METACLASMATOCOLEA** Engel, subg. nov.

Folia caulina indivisa, integra; amphigastria principalis axis vel rami laterales intercalares inconspicui, reducti, squamiformi, polymorphi.

Type species: *Clasmatocolea navistipula* (Steph.) Grolle.

Lateral-intercalary branches often copiously developed, *Frullania*-type branching rare; leaves undivided, entire; underleaves of main axis and/or lateral-intercalary branches inconspicuous, reduced, scalelike, polymorphous, often of only a few cells.

Distribution.—Southern South America.

Sect. **PUCCIOANAE** Engel, sect. nov.

Haec amphigastria caulina principalis axis bene manifesta, illa ramorum lateralorum intercalarorum inconspicua atque reducta; rami laterales intercalarores copiose effecti, incrementi parvi, plerumque abbreviati.

Type species: *Clasmatocolea puccioana* (De Not.) Grolle.

Underleaves of main axis well developed, those of lateral-intercalary branches inconspicuous and reduced; lateral-intercalary branches copiously produced, of limited growth, usually abbreviated.

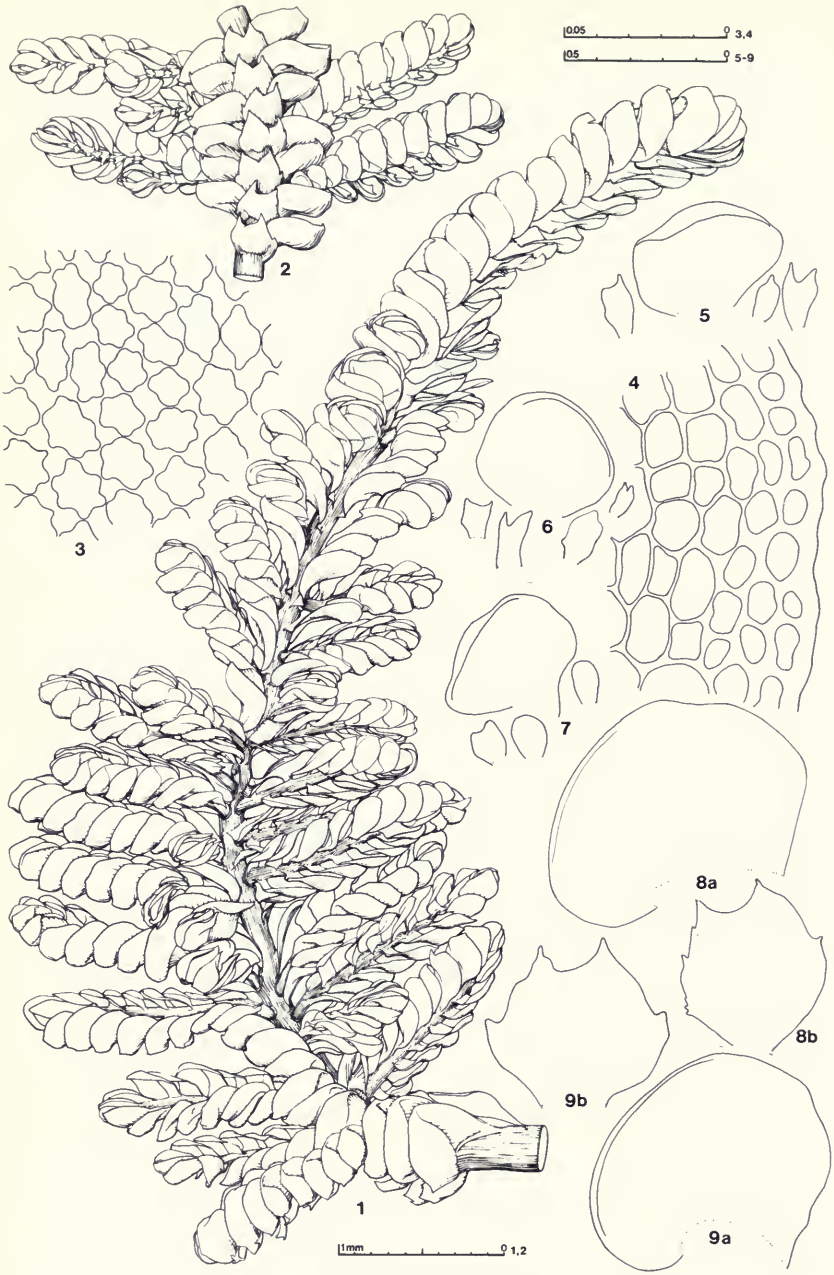
Distribution.—Southern South America.

Clasmatocolea puccioana (De Not.) Grolle. Figures 49-51, Plates 23-25.

Jungermannia ?puccioana De Not. Mem. Reale Accad. Sci. Torino II. 16:221. *pl. IX, 1-6.* 1855. *Lophocolea puccioana* (De Not.) Mass. Nuovo Giorn. Bot. Ital. I. 17:227. 1885. *Lophocolea puccioana* a* forma *primigenia* Mass. Nuovo Giorn. Bot. Ital. I. 17:227. 1885. *Lophocolea puccioana* var. *β primigenia* (Mass.) Schiffn. *in* Naumann, Forschungsr. *Gazelle* 4 (4):13. 1889. *Clasmatocolea puccioana* (De Not.) Grolle, Rev. Bryol. Lichénol. 29:72. 1960. Original material: Chile, "Prov. Valparaíso, Valparaíso," *Puccio* (*non vidi;* GE = O, NY = O, PAD = O, PG = O, RO = O, TO = O).

Opposite:

FIG. 48. *Clasmatocolea tjiwideiensis* (Sande Lac.) Grolle. **1-2,** Main axis, lateral view (note position of leaf dentition). **3,** Main axis, ventral-lateral view. **4,** Main axis, showing leaf and underleaf insertion, ventral view. **5, 6,** Underleaves. **7-9,** Leaves (flattened). **10,** Stem, cross section, note irregularly shaped cell lumina. **11,** Median leaf cells with cuticular papillae indicated by stipple; three secondary cell wall thickenings indicated. **12-14,** Teeth from ventral-basal portion of leaf, with cuticular papillae indicated. Figures 1-3, 6-14, from type of *Chiloscyphus tjiwideiensis*, *Junghuhn*, Java; figures 4, 5, from *Kurz s. n.*, Java.


0.05
3,4
0.5
5-9
2
5
4
3
6
7
8a
8b
9b
9a
1
1mm
1,2

Lophocolea diversistipa Steph. Kongl. Svenska Vetenskapsakad. Handl. 46 (9):42. *f. 15 e, f.* 1911, *syn. fide* Engel (1978). Original material: Chile, Prov. Magallanes, Pto. Gray, 7 June 1908, *Skottsberg 198* (UPS! — c. per.); Pto. Ramirez, *Halle* and/or *Skottsberg* (*non vidi*); Pto. Cutter, 13 April 1908, *Halle & Skottsberg 198* (UPS!).

Lophocolea patagonica Beauv. *in* Steph. Spec. Hep. 6:572. 1924 *ut nom. nov. pro Lophocolea rotundistipula* Steph. Kongl. Svenska Vetenskapsakad. Handl. 46 (9):52. *f. 20 a-e.* 1911, *syn. fide* Engel (1978) *non L. rotundistipula* Steph. Bull. Herb. Boissier 6 (9):793. 1906 (= Spec. Hep. 3:93). Original material: Chile, Prov. Magallanes, F. Peel, 16 June 1908, *Skottsberg s. n.* (UPS!).

Plants prostrate, commonly mixed with other bryophytes, occasionally in ± pure tufts, *light brown-sienna, stems often rather deep orange-brown; main axes 560-910 μ wide.*

Branches copiously developed, somewhat less copious in very elongated axes; *lateral-intercalary type in great abundance, much narrower in width than main axis, the branches short, of limited growth, subvermiform*, sometimes ± erect, *delicate, usually not in turn branched*, often originating from near ventral end of insertion of associated leaf, the lateral-intercalary branches sporadically becoming leading axes with their own copiously developed short, lateral-intercalary branches (this leading axis may, in turn, produce another leading axis); *ventral-intercalary branches very rare* (2 seen), like lateral-intercalary branches; Frullania-*type branches rare.*

Stems 9-12 cells high, cortex in 2-3 rows of *very thick-walled cells* smaller than, or ca. equal in size to the medullary cells, the exposed wall of outer row very thickened; medullary cell walls thin to slightly thickened, with corners thickened as in medium trigones; endophytic hyphae present in both cortex and medulla. Rhizoids frequently present, rather long, in fascicles from stem near underleaf base.

Leaves with insertion distinctly recurved at ventral end; leaves erect to slightly spreading, occasionally connivent dorsally, loosely imbricate, conchiform concave, *suboblate to subreniform to broadly ovate;* apex broadly rounded to truncate, undivided, *entire*, exceptionally with a single large tooth; *margins entire;* dorsal margin ± straight in proximal half, sinuous; ventral margin broadly rounded, sometimes somewhat incurved, usually extending ventrally beyond stem and nearly but usually not in contact with underleaf. *Intercalary branch leaves* 0.25-*0.5 the size of the leaves*, often slightly more closely imbricate than in main axis, *entire.*

Opposite:

FIG. 49. *Clasmatocolea puccioana* (De Not.) Grolle. **1,** Main axis showing lateral-intercalary branching pattern. **2,** Lateral-intercalary branches and adjacent main axis. **3,** Median leaf cells. **4,** Stem, cross section. **5-7,** Leaf and underleaves from *lateral-intercalary branches.* **8-9,** Leaf and underleaf from *main axis.* Figures 1, 2, from *Engel 4272B*, Chile, Prov. Aisén, Pto. Island; figures 3, 8, from *Skottsberg 198*, Chile, Prov. Magallanes, Pto. Gray (syntype of *L. diversistipa*); figure 4, from *Engel 4520*, Chile, Prov. Magallanes, Pto. Edén; figures 5, 9, from *Engel 4515*, Chile, Prov. Magallanes, Pto. Edén; figure 6, from *Engel 4385A*, Chile, Prov. Aisén, F. Témpano; figure 7, from *Engel 5248D*, Chile, Prov. Magallanes, I. Juan.

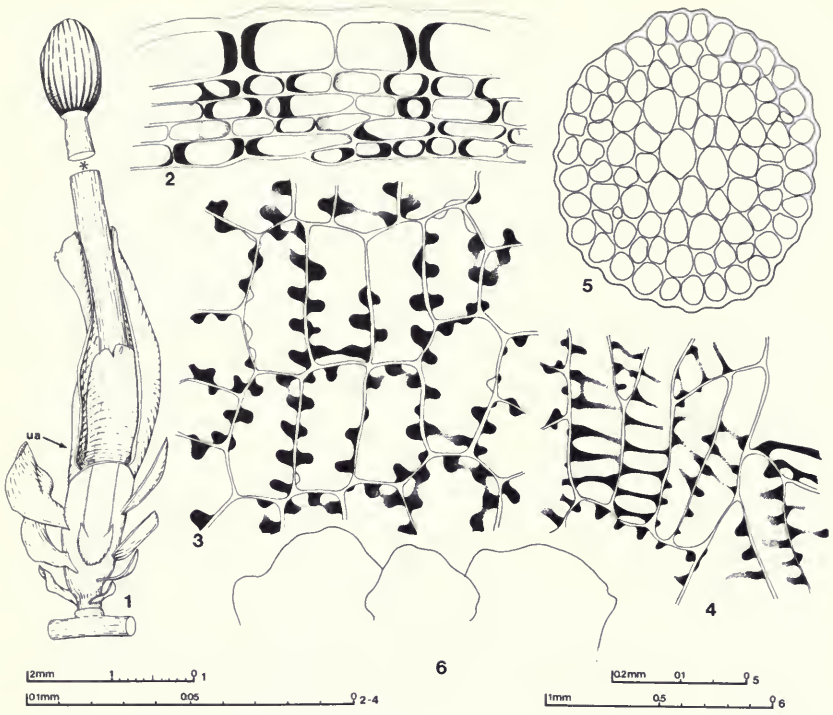


FIG. 50. *Clasmatocolea puccioana* (De Not.) Grolle. **1,** Gynoecium on abbreviated lateral-intercalary branch; lower portion an oblique longitudinal section, upper portion with merely a portion of perianth removed; note position of unfertilized archegonia (ua) and bracts. **2,** Capsule wall, cross section. **3,** Outer capsule wall cells. **4,** Inner capsule wall cells. **5,** Seta, cross section. **6,** Perianth mouth, ventral lobe in middle. Figures 1, 4, 5, from *Engel 4541*, Chile, Prov. Magallanes, Pto. Edén; figures 2, 3, from *Engel 4520*, Chile, Prov. Magallanes, Pto. Edén; figure 6, from *Engel 5361B-2*, Chile, Prov. Magallanes, B. Wide.

Leaf cells thin to moderately thick-walled, the *trigones large and moderately bulging to coarse and nodular*, often confluent, commonly with leaf cell lumen, except for narrow thin-walled places, bounded mostly by the massive trigones; median leaf cells 11-20 μ wide, 12-24 μ long; cuticle smooth.

Underleaves 1.2-3.0 × stem width, free, moderately spreading, approximate, moderately convex (ventral view), elliptic to ovate to oblate; *apices bidentate to broadly retuse to bifid to 0.2(-0.25)*, the segments of similar size and shape, very often apiculate, the segments or teeth at apex terminating in a slime papilla, the segment margins entire; margins of the lamina entire or median or median-basal portion with 1 small to large tooth or small lobe and occasionally a slime papilla, the margins rarely with 2 teeth, the armature terminating in a slime papilla. Underleaves of small, copiously produced intercalary branches, *small, commonly inconspicuous, strongly spreading, often spreading to 90° or slightly to moderately recurved; underleaves polymorphous*, ovate to elliptic to

subrectangular to ± cuneate to obovate, the *lamina often of only a few cells high; apices undivided or with a single tooth or lobe, sometimes bifid; lobes or teeth often asymmetric*, terminating in a slime papilla, often with 1 lobe large and conspicuous and other lobe reduced to a tooth or slime papilla; *lamina margins entire or with 1 tooth* or slime papilla; underleaves of somewhat larger intercalary branches nearer to configuration of main axis underleaves.

Plants dioecious; androecia on short, abbreviated lateral-intercalary branches, rarely terminal or intercalary on main axis or robust, well-developed lateral-intercalary branches; bracts with basal portion strongly saccate and distal portion strongly concave, the apices appressed to bract immediately above; lobule margin involute, with a rounded lobe possessing 1 tooth and/or a few slime papillae; antheridia solitary, the stalk uniseriate.

Gynoecia on short to rather long lateral-intercalary branches; subfloral innovations absent; vestigial stem perigynium present; bracts in 3-4 series, the bracts and bracteoles of innermost and third series inserted on the vestigial perigynium; bracts of innermost series slightly concave to slightly convex, broadly obovate to subrectangular; apices undivided, broadly rounded to truncate, entire; margins occasionally sinuous, occasionally reflexed, entire or with 1-few teeth. Bracteoles of innermost series subequal to or slightly smaller than bracts in size, free from bracts; bracteoles moderately concave to subcanaliculate (ventral view), broadly obovate to suboblate to subrectangular; apices undivided, broadly rounded, bidentate or with 2 slime papillae; lamina margins sometimes sinuous, with low, rounded projections or short, blunt lobes, the margins entire or occasionally with a few teeth. *Perianth trigonous, narrowly ovate to elongate-rectangular*, the ventral side slightly to strongly infolded nearly throughout, and then lending perianth ± bilaterally compressed, or ventral side straight or slightly convex in median and basal portions and infolded in apical portion; perianth sides narrowing toward the ± bilaterally compressed mouth; lobes broadly rounded, *often with low, rounded projections*, the *lobes entire or with a few teeth;* keels in apical region along with the adjacent portion of the lobe often sharply recurved or incurved; keel wings sometimes present, of several cells high and sometimes with an auriculate appendage. Calyptra large.

Seta 6-10 cells in diameter, with 28-33 rows of outer cells; median core cells larger than "epidermal" cells, the core cells becoming smaller toward periphery, with the outermost 1(-2) rows of core cells ca. equal to or slightly smaller than "epidermal" cells; core cells with corners thickened similarly to small to medium trigones. Capsule narrowly elliptic to ovoid, the valves 0.74-1.37 mm. long, of 36-42 μ thick, of 4-5(-6 locally) layers, the outer layer of cells *equal to thickness of (2.5-)3.0-3.9 of interior strata;* outer layer with vinaceous or red-brown, nodule-like or occasionally spinelike thickenings that are often feebly tangentially dilated, semiannular bands occasional; exposed wall of outer layer thickened; intermediate and inner layers subequal in size or with outermost intermediate layer thicker than inner layer of capsule, the intermediate layers with thickenings often considerably extending onto tangential walls, semiannular bands occasional; inner layer with red-brown semiannular bands moderately to very common, nodulose thickenings very common.

Spores 11-12(-13) μ, light brown, exine with the light microscope appearing minutely punctate, but under the SEM with a network of short, wide vermiform ridges covered with sometimes coalescing nanogranules, the intervening walls with several, rather close nanogranules; spores averaging 1.5 × elater diameter. Elaters 7-9 μ wide, apical portions often with thick nonspiral walls; elater walls red-brown.

Variation.—The branch underleaves of *C. puccioana* and those of the main axis of *C. navistipula* are of comparable shape and tend to have similar variability of underleaf segments.

Differentiation.—Clasmatocolea puccioana is closely related to *C. navistipula;* see the discussion (p. 171) under the latter for distinguishing the two taxa. *Clasmatocolea puccioana* shows some relationships to *C. fulvella ;* for a discussion, see that species.

The primary distinctive features that will distinguish this species from all other members of the genus are those of branching patterns and branch characteristics; these are (a) the copiously developed lateral-intercalary branches that are much narrower in width than the main axis and that are short, of limited growth, subvermiform, delicate, and usually not in turn branched; (b) the distinctive intercalary branch underleaves that are small, commonly inconspicuous, sometimes with a lamina of only a few cells high, strongly spreading, and with polymorphous apices and outline; and (c) the rarity of *both* ventral-intercalary and *Frullania*-type branching.

Significant supplementary distinctive features are the 2-3-layered very thick-walled cortex and the light brown-sienna color. The quite characteristic color of this species can be used to identify it at a glance when the species is mixed with other *Clasmatocolea* taxa such as *C. navistipula* or *C. obvoluta.*

Notes.—1. Based upon the study of syntypes from all localities listed in Stephani (1911), *Lophocolea diversistipa* is a synonym of *C. puccioana.* In his original description, Stephani states that the plants are pale light green in color, and the branches are clustered. The specimens from Puerto Ramirez are misdeterminations of *C. humilis*, are light brown in color, and are sparingly branched. The specimens from Puerto Gray and Puerto Cutter, however, are *C. puccioana* and are light green to yellow-green in color and have numerous lateral-intercalary branches. Further, the Puerto Gray and Puerto Cutter specimens have underleaves with sinuses of the shapes given in Figures 15e and f of Stephani (1911), *i.e.*, bifid to ca. 0.5 and widely triangular and bifid to less than 0.3 and rounded, respectively. Because these three characters are referable to plants identifiable as *C. puccioana*, *Lophocolea diverstipa* is included in its synonymy.

Stephani (1922, p. 270) cannot be used for aid in typification, because he states the leaves are to 0.25-divided, a character not present in either *C. humilis* or *C. puccioana.* There is a Skottsberg collected specimen in G (No. 14135) labeled "*Lophocolea diversistipa*, Patagonia australis," that is actually *Acrobolbus ochrophyllus.* It is possible that Stephani utilized this plant in a portion of his description of *Lophocolea diversistipa*, because he states for the stem, "cuticla papillata," for the leaves "apice

FIG. 51. *Clasmatocolea puccioana* (De Not.) Grolle.

ad 1/4 inciciso-biloba sinu recto lobis late triangulatis" and "cuticula dense minuteque papillata," all of which are characters of *A. ochrophyllus*. [Characters of the underleaves are seemingly those of *L. diversistipa* = *C. puccioana*, although they vary from those used in Stephani (1911).] It is possible that Stephani distributed that portion of the original material of *Lophocolea diversistipa* utilized for the protologue of this species in Stephani (1911), retaining only material of *A. ochrophyllus* (which *may* have been an admixture) and then using this plant for the description in *Species Hepaticarum*.

2. *Clasmatocolea puccioana*, like several other members of the genus, has a vestigial stem perigynium on which several series of bracts and bracteoles are inserted. The phenomenon in *C. puccioana* seems to be closely related to the occurrence of fertilization.

3. Reports of *C. puccioana* from the Falkland Is. are based upon misdeterminations of *C. fulvella*. Reports of *L. puccioana* in Stephani (1900, 1901) and Herzog (1939, 1954) are based upon misdeterminations of *C. humilis*. The record of *L. puccioana* in Arnell (1955a), plus many of Santesson's collections labeled *L. puccioana* are actually *C. gayana*.

Ecology.—In forests where on fallen trees and in layers of vegetation over logs. The species also occurs on the sides and apices of rather exposed bryophyte mounds, where often mixed or associated with *Blepharidophyllum densifolium*, *Acromastigum* sp., and *Plagiochila* sp. Also in moorland areas where on cliffs or over soil. It is rather common in *Sphagnum* moors.

Phytogeography.—Tierra del Fuego (I. de los Estados and wet, cold, southern Chilean islands); Patagonian Channels N. to 48° 04′ S.; also at 1,000 m. in Cord. Pelada (40° 07′ S., El Mirador, Prov. Valdivia) (see fig. 51).

Specimens seen.—**ARGENTINA.** TERR. TIERRA DEL FUEGO: I. de los Estados, Pto. Cook, *Skottsberg s.n.* (hb. Grolle). **CHILE:** *Sin. loc.*, *Poeppig s.n.* as *Chiloscyphus notophyllus* (BM). PROV. MAGALLANES: S. Darwin, *Spegazzini s.n.* as *Chiloscyphus notophyllus* (BM); I. Chair, *Spegazzini 253* (VER); I. Burnt, Cabo Desolación, *Spegazzini 261* (VER); I. Basket, *Spegazzini s.n.* as *Lejoscyphus turgescens* (NY); S. Melville (not I. Melville), M. Skyring, *Spegazzini 29b* (VER); I. Capitan Arecena ("I. Clarence"), *Hariot 7, 27* (VER); B. Tuesday, *Naumann s.n.* (FH); Brunswick Pen. (cf. Engel, 1978); E. side of B. Borja, *Engel 6144B, 6163B* — c. per. (MSC); E. side of Pto. Bueno, *Engel 5589* — c. ♂ (MSC); F. Peel, *Skottsberg s.n.* as syntype of *L. rotundistipula* (UPS); I. Chatham, B. Wide, *Engel 5361B-2* — c. per. (MSC); E. side of I. Juan, *Engel 5248D*

(MSC); W. side of I. Grant, *Engel 4705D* (MSC); Pto. Alert, *Engel 4913* — c. sporo. (MSC); ibid., head of fiord W. of M. Markham, *Engel 4959* — c. sporo., *4990A* — c. per. (MSC); Pto. Grappler, *Skottsberg s.n.* (hb. Grolle); Pto. Edén, *Engel 4515*, *4520* — c. sporo., *4522* — c. ♂, *4528* — c. ♂, *4532A* — c. ♂, *4533* — c. ♂, *4541* — c. sporo. + ♂ (MSC); B. Halt, *Cunningham s.n.* (NY); ibid., *Cunningham 95* as *Chiloscyphus notophyllus* (BM). PROV. AISÉN: N. side of F. Témpano, *Engel 4385A* — c. per., *4399B* — c. ♂ (MSC); Pto. Island, *Engel 4272B* — c. per., *4311* (MSC). PROV. VALDIVIA: Cord. Pelada, summit of El Mirador, between La Union and Pta. Hueicolla, 1,000 m., *Engel 12371*, *12376* (F).

Sect. METACLASMATOCOLEA

Lateral-intercalary branches usually of unlimited growth; underleaves of both main axis and branches reduced, those of main axis frequently with asymmetric segments; male bracts conduplicately bilobed.

Distribution.—Southern South America.

Clasmatocolea navistipula (Steph.) Grolle. Figures 52-54, Plates 26, 27.

For synonymy see under varieties.

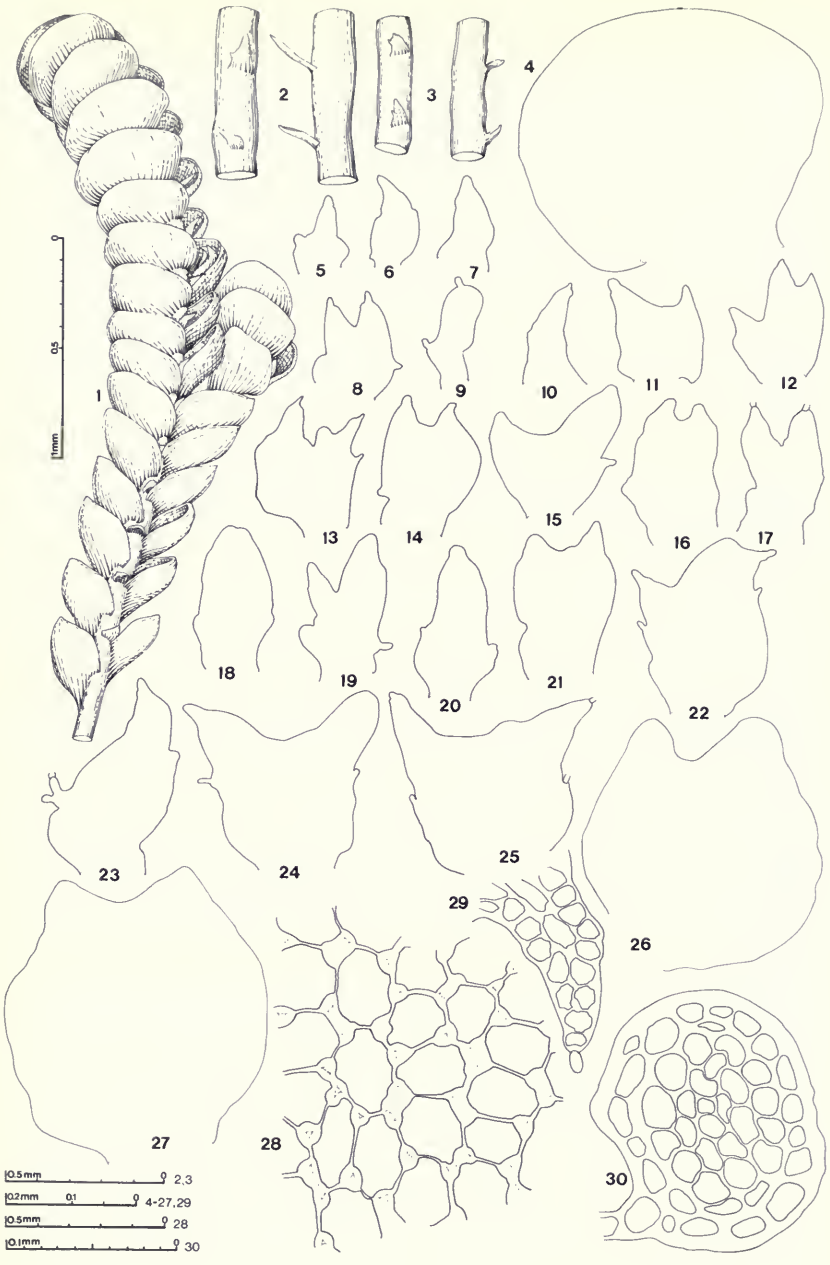
Plants *delicate*, *spongy*, prostrate to suberect, *in very compact*, *pure mats*, less often mixed with other hepatics, *whitish-pale green to pale grey-green*, sometimes tinged with red-brown; *main axes 455-595 μ wide*.

Branches copious, *lateral-intercalary type abundant*, *ventral-intercalary type occasional*, Frullania-*type rare;* branches often arising from a leafless main axis, the *branches very often long and of unlimited growth*, often exceeding length of main axis, which usually remains quite short, the branches often in turn branched or repeatedly branched; branches slightly to moderately narrower than main axis; terrestrial plants with branching pattern very often rather narrowly to broadly flabellate; aquatic or subaquatic plants with only a few branches.

Stems 6-10 cells high, cortex in 1-3 rows of moderately thick-walled cells larger than, slightly smaller than, or ca. of same size as medullary cells; exposed wall of outer cortical row moderately to very thickened; medullary cell walls increasing in size toward stem periphery, the outermost cells subequal to cortical cells, the medullary cell walls slightly to moderately thickened and with corners thickened similarly to small trigones; endophytic hyphae absent or present in cortex or both cortex and medulla. Rhizoids long for plant size, in ill-defined areas at and near underleaf bases, but several scattered along ventral surface of stem, especially near the leaf insertion.

Leaves (main axis) often caducous or partially decayed, the insertion very slightly recurved at ventral end; leaves erect, rarely dorsally connivent, contiguous to loosely imbricate, conchiform concave, ± *reniform to oblate;* apex broadly rounded to truncate, undivided, *the apex and margins entire;* dorsal margin ± straight in proximal half, frequently slightly recurved, the ventral margin broadly rounded.

Leaf cells thin walled, *trigones large to bulging to* (*mostly*) *nodular and protuberant*, often confluent; median leaf cells 13-25 μ wide, 17-31 μ long; cuticle smooth or slightly


1
0
0.5
1mm
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
0.5mm 2,3
0.2mm 0.1 4-27,29
0.5mm 28
0.1mm 30

roughened and appearing finely granular. Oil-bodies throughout leaf, occupying small fraction of cell lumen, hyaline, glistening, of grape-cluster type, with numerous, *bulging globules* of 1-2 μ in diameter, the oil-body surface appearing coarsely botryoidal, the segmentation distinct; oil-bodies globose to ovoid to elliptic in shape, consistently 2 per cell of leaf middle and apex, 2-4 of leaf base, those of leaf middle 5 μ wide, 9-11 μ long.

Underleaves often caducous, 0.46-1.7 × stem width, often covering only a fraction of stem tissue, sometimes becoming very reduced and inconspicuous toward main axis apices, the underleaves free or weakly connate on 1 side, *moderately to rather strongly spreading, distant, ± plane, polymorphous:* narrowly triangular to ovate to elliptic to subrectangular to cuneate; *apices undivided or bifid; segments* (when present) *often of different size and configuration, often widely spreading and separated by a lunate sinus;* segments or undivided underleaf apex terminating in a slime papilla; segment margins entire or (rarely) with 1 tooth; *lamina margins entire or with 1-2 teeth* or slime papillae. *Branch underleaves very reduced, very inconspicuous, strongly spreading*, sometimes recurved, *variable in size and shape, some* (especially those of 2nd, 3rd, and 4th order) *of only a few cells and then scalelike, undivided, and ± narrowly triangular*, whereas *others are somewhat larger and sublanceolate;* underleaves of branches sporadically large, and then are occasionally short-bifid and with lobes or teeth often asymmetric.

Plants dioecious; androecia terminal or intercalary on lateral-intercalary branches of varying lengths; bracts with basal portion strongly saccate and distal portion strongly concave, with the often subcrenulate apices appressed to bract immediately above; *bracts conduplicately bilobed*, the lobule *small, elliptic to narrowly ovate, attached for varying lengths to adaxial surface of lobe*, the lobule sometimes smaller and lanceolate; antheridia 1(-2) per bract, the stalk uniseriate or very locally biseriate.

Gynoecia on rather short or abbreviated lateral- or ventral-intercalary branches; subfloral innovations absent; *vestigial stem perigynium present; bracts and bracteoles of innermost 2 or all 3 series inserted on the stem perigynium;* bracts of innermost series concave, ovate to ovate-wide subrectangular, and closely adhering to perianth; bract apices rather narrowly to broadly rounded, undivided, entire; lamina margins sometimes recurved, entire or with 1 slime papilla. Bracteoles of innermost series free from bracts, plane, ovate to elongate-subrectangular to narrowly triangular; apices poly-

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Opposite:

FIG. 52. *Clasmatocolea navistipula* (Steph.) Grolle. **1,** Lateral-intercalary branch, with two young, secondary lateral-intercalary branches, ventral-lateral view. **2, 3,** Ventral and lateral views of same lateral-intercalary branch. **4,** Leaf of long leading lateral-intercalary branch. **5-27,** Underleaves. **28,** Median leaf cells. **29,** Underleaf of large, leading lateral-intercalary branch. **30,** Stem, cross section. Figures 1, 4, 7, 10, 28, 29, from type of *L. navistipula*, *Dusén 155*, Chile, Prov. Magallanes, I. Desolación; figure 2, from *Engel 2129-1*, Chile, Prov. Magallanes, Pto. Cutter; figure 3, from *Engel 6127*, Chile Prov. Magallanes, B. Borja; figures 5, 8, 16, from *Engel 5357*, Chile, Prov. Magallanes, B. Wide; figures 6, 21, 30, from *Engel 4251*, Chile, Prov. Aisén, Pto. Island; figures 9, 12, 13, 19, from *Crow 1472*, Argentina, Terr. Tierra del Fuego, Tierra Mayor Valley; figures 11, 14, 15, from *Engel 6175*, Chile, Prov. Magallanes, B. Borja; figure 17, from *Engel 4822*, Chile, Prov. Magallanes, Pto. Charrúa; figures 18, 20, from *Engel 4366*, Chile, Prov. Aisén, F. Tempano; figures 22-25, 27, from *Engel 2105*, Chile, Prov. Magallanes, La. El Parrillar region; figure 26, from *Engel 6425*, Chile, Prov. Magallanes, between B. Bougainville and B. San Nicolas. (Figures 9, 12, 13, 19, 22-27 are of **var. parceramosa**).

1
2
3
4
5
6
7
8
9
10
11
2mm
1
1·6
0,5 mm
8,9
1mm
0,5
7
0,5 mm
10,11

morphous: undivided and truncate or acutely angular or narrowly rounded, or bifid to 0.30; lamina margins entire or with 1 small lobe. Perianth obscurely to moderately trigonous, *rather strongly inflated in median and basal portions, but with upper portion somewhat bilaterally compressed* (the perianths rather inflated throughout when young, but often somewhat collapsing toward apex at maturity); perianth falcate-elliptic to subcylindrical to ovoid to clavate, commonly narrowing toward the *weakly opened or closed, somewhat bilaterally compressed mouth;* lobes often incurved or inrolled, broadly rounded, the *ventral considerably smaller*, the *lobes entire* or with a few slime papillae, occasionally sinuate.

Seta 6 cells in diameter, with 15-16 rows of outer cells surrounding an inner core of scattered, smaller cells with corners thickened similar to medium trigones. Capsule elliptic, the valves 0.88-0.98 mm. long, 42-48 μ thick, of 4-5 layers, the outer layer of cells 18-25 μ thick, equal to thickness of 3 of interior strata or outer layer greater than diameter of all interior strata combined; outer layer with very pale brown or hyaline or red-brown, nodule-like to wide spinelike thickenings that are tangentially dilated, a few semiannular bands present; exposed wall of outer layer moderately thickened; intermediate strata with outermost layer thicker than inner layer of capsule, the intermediate layers with thickenings often considerably tangentially dilated; inner layer of cells (5-)6-8 μ thick, with pale brown or red-brown semiannular bands very common, the bands often incomplete, nodular thickenings occasional.

Spores 11-12 μ, light brown, exine with the light microscope appearing minutely punctate, but under the SEM with coarsely granulate to short, abbreviated, wide, vermiform projections that occasionally have nanogranules; spores averaging 1.5 $\times$ elater diameter. Elaters 7-8 μ wide, apical portions occasionally with thick nonspiral walls; elater walls red-brown, 2(-3) μ in diameter.

KEY TO VARIETIES OF *Clasmatocolea navistipula*

1. Branching copious, in a narrow to broad flabellate pattern, *Frullania*-type branching absent; underleaves to 0.95 $\times$ stem width; plants on rotted stumps or logs or on soil ..... var. *navistipula*
1. Branching sparingly developed, not copiously produced and never in a flabellate pattern, *Frullania*-type branching occasionally present; underleaves to 1.7 $\times$ stem width; plants of pools, pool margins, or *Sphagnum* bogs ..... var. *parceramosa*

Clasmatocolea navistipula (Steph.) Grolle, var. **navistipula.**

Lophocolea navistipula Steph. Bull. Herb. Boissier 6 (7):543. 1906 (= Spec. Hep. 3:57). *Clasmatocolea navistipula* (Steph.) Grolle,

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Opposite:

FIG. 53. *Clasmatocolea navistipula* (Steph.) Grolle. **1, 2,** Diagrammatic representation of branching pattern of **var. navistipula. 3-6,** Diagrammatic representation of branching pattern of **var. parceramosa. 7,** Perianth mouth, ventral lobe in middle (lobe to left has 3 slime papillae). **8, 9,** Mature perianth, cross section through median portion. **10, 11,** Male bracts, adaxial view. Figure 1, from *Engel 5357*, Chile, Prov. Magallanes, B. Wide; figure 2, from *Engel 2129-1*, Chile, Prov. Magallanes, Pto. Cutter; figures 3-6, from *Engel 6425*, Chile, Prov. Magallanes, between B. Bougainville and B. San Nicolas; figures 7, 9, from *Engel 6127*, Chile, Prov. Magallanes, B. Borja; figure 8, from *Engel 1856*, Chile, Prov. Magallanes, R. San Juan; figures 10, 11, from *Engel 4822*, Chile, Prov. Magallanes, Pto. Charrúa.

FIG. 54. *Clasmatocolea navistipula* (Steph.) Grolle. ● = var. *navistipula*; ○ = var. *parceramosa*.

Feddes Repert. 82 (1):88. 1971. Original material: Chile, Prov. Magallanes, I. Desolación, (Pto. Angosto), *Dusén* (FH! – c. ♂, G!).

Jamesoniella difficilis Steph. Kongl. Svenska Vetenskapsakad. Handl. 46 (9):17. *f. 6 a.* 1911, *syn. fide* Grolle (1971). Original material: Chile, Prov. Magallanes, Pto. Grappler, *Skottsberg* (BM!, UPS!); I. Atalaya, *Halle* and/or *Skottsberg* (*non vidi*); S. Skyring, B. Rodriguez, *Halle & Skottsberg* (hb. Grolle!, S! UPS!); Canal Gajardo, V. Inga, *Halle* and/or *Skottsberg* (*non vidi*); B. Arauz, *Halle* and/or *Skottsberg* (*non vidi*); W. end of L. Fagnano, *Skottsberg* (UPS!).

Lophocolea subcapillaris Steph. Kongl. Svenska Vetenskapsakad. Handl. 46 (9):54. *f. 18 e, f.* 1911, *syn. fide* Engel (1978). Lectotype (*fide* Engel, 1978): Chile, Prov. Magallanes, R. Fontaine, 1 March 1908, *Halle & Skottsberg 234* (UPS!).

Branching copious, in a narrow to broad flabellate pattern, *Frullania*-type branching absent; underleaves to 0.95 × stem width.

Differentiation.—*Clasmatocolea navistipula* is a rather close ally of *C. puccioana*, which also has lateral-intercalary branches profusely developed and branch underleaves reduced and inconspicuous. Plants of *C. navistipula* may be differentiated from the latter by the following features: (a) the reduced *main axis* underleaves that often cover only a small fraction of stem tissue; (b) the frequently asymmetric segments of main axis underleaves (*i.e.*, underleaves with one segment smaller than the other; see below); (c) the often unlimited growth of the lateral-intercalary branches; (d) the branch underleaves that are considerably more reduced than those of the short, lateral-intercalary branches of *C. puccioana*;[9] (e) the conduplicately bilobed male bracts; (f) the whitish-light green color; and (g) the narrower axis width (455-595 μ). Further, the flabellate branching pattern developed in the typical variety is lacking in *C. puccioana*.

The androecia are unique within the genus. The bracts are conduplicately bilobed, with the dorsal, basal portion of the bract with a small, elliptic to narrowly ovate lobule attached to its adaxial surface for varying lengths. Sometimes the lobule is rather inconspicuous and in such cases should be searched for with care.

Notes.—1. The main axis, the underleaves of which I have used as a key character, may not be obvious due to copious branching, and the main axis should then be carefully searched for and identified by the comparatively large underleaves (0.46-1.7 × the main axis width) and the slightly

[9] Underleaves of branches of both *C. puccioana* and *C. navistipula* may best be observed by removing the leaves and viewing the branch with the light microscope.

wider axis width. The main axis can often be recognized by its age, for as the copious branches become better developed, the main axis becomes brown and looses its leaves and underleaves.

2. Stephani (1911), in his description and drawings of *Lophocolea subcapillaris*, was clearly not referring to the syntypes from Insula Pacheco, which are misdeterminations of *Hepatostolonophora abnormis* (Besch. & Mass.) Engel & Schust., and a Río Fontaine plant was therefore selected as a lectotype.

Ecology.—The two varieties of *C. navistipula* are ecologically distinct; the typical variety grows on rotted stumps or logs and over soil. In the Patagonian Channel region on well-decayed logs in forests; less commonly on *Pilgerodendron* bark and in thick masses of epiphytic vegetation over tree trunks (see Engel, 1978).

Phytogeography.—Tierra del Fuego; Patagonian Channels; in Valdivian region N. to 36° 50′ S. (Prov. Concepción) (see fig. 54).

Specimens seen.—**CHILE.** PROV. MAGALLANES: *Sin. loc.* [probably W. end of L. Fagnano], *Skottsberg s.n.* as syntype of *J. difficilis* (G); Cta. Barrow, *Skottsberg 231* as *L. subcapillaris* (UPS); Brunswick Pen. (cf. Engel, 1978); E. side of B. Borja, *Engel 6127* — c. sporo., *6175*, *6205* (MSC); S. Skyring, B. Rodriguez, *Halle & Skottsberg 220* (UPS); I. Chatham, N. shore of B. Wide, *Engel 5357* (MSC); Pto. Charrúa, head of inlet, *Engel 4822* — c. ♂ (MSC); Pto. Alert, at head of fiord W. of M. Markham, *Engel 4961B* — c. ♂, *4965* — c. sporo. + ♂ (MSC); Can. Messier, Port Grappler, *Skottsberg 220* (S, UPS). PROV. AISÉN: N. side of F. Témpano, *Engel 4366* (MSC); Pto. Island, *Engel 4251* — c. sporo. + ♂ (MSC). PROV. VALDIVIA: V. Shoshuenco, *Ruthsatz 44/18* (hb. Grolle). PROV. CONCEPCIÓN: Concepción, *Dusén 155* as *L. puccioana* (NY). Patagonia: *Sin. loc.*, *Skottsberg 585*, *807* as syntype of *J. difficilis* (G).

Clasmatocolea navistipula var. **parceramosa** Engel.

Clasmatocolea navistipula var. *parceramosa* Engel, Phytologia 41:311. 1979. Holotype: Chile, Prov. Magallanes, Brunswick Pen., ridge between B. Bougainville and B. San Nicolas, 9 October 1969, *Engel 6425* (MSC!).

Branching sparingly developed, non-flabellate, *Frullania*-type branching occasionally present; underleaves to 1.7 × stem width.

Ecology.—The two varieties of *C. navistipula* occur in separate and distinct ecological niches; var. *parceramosa* occurs in pools, pool margins or *Sphagnum* bogs.

Phytogeography.—Southern South America at I. Grande de Tierra del Fuego and southern Patagonian Channels (Brunswick Pen.) (see fig. 54).

Specimens seen.—**ARGENTINA.** TERR. TIERRA DEL FUEGO: Tierra Major Valley, near junction of Ruta Nac. No. 3 with Harberton road (Ruta J), 240 m., *Crow 1472* (MSC). **CHILE.** PROV. MAGALLANES: Brunswick Pen., near E. shore of La. El Parrillar, ca. 365 m., *Engel 2105* (MSC); Brunswick Pen., ridge between B. Bougainville and B. San Nicolas, ca. 155 m., *Engel 6444A* — c. per. + ♂ (MSC).

Subg. **SQUAMICALYX** Engel, subg. nov.

Folia caulina indivisa, integra; cellulae foliorum trigonae graves, protuberantes, saepe confluentes; amphigastria caulina utrinque connata; bracteolae involucraliae utrinque connatae; perianthium habens magnas squamas.

Type species: *Clasmatocolea notophylla* (Hook. f. & Tayl.) Grolle.

Leaves undivided, entire; trigones massive, protuberant, often confluent; underleaves connate on both sides, moderately to distinctly cupulate, undivided; bracteoles connate with bracts on both sides; perianth with large scales.

Distribution.—Amphipacific; New Zealand and its subantarctic islands, Tasmania, southern South America.

Clasmatocolea notophylla (Hook. f. & Tayl.) Grolle. Figures 55, 56.

Jungermannia notophylla Hook. f. & Tayl. London J. Bot. 3:376. 1844. *Chiloscyphus notophyllus* (Hook. f. & Tayl.) G. L. & N. Syn. Hep. 710. 1847. *Lophocolea notophylla* (Hook. f. & Tayl.) Hodgs. *in* Martin, Trans. & Proc. Roy. Soc. New Zealand 78:495. 1940. *Clasmatocolea notophylla* (Hook. f. & Tayl.) Grolle, J. Jap. Bot. 41:228. 1966. Original material: Auckland Is., *Hooker* (FH—hb. Steph.!, L!, LD!, NY!, S!).

Lophocolea tumida Steph. Bull. Herb. Boissier 6 (9):791. 1906 (= Spec. Hep. 3:91), *syn. fide* Grolle (1966). Holotype: Tasmania, Mt. La Perouse, *Oldfield* (G! — c. per.; isotypes: FH! — c. per., JE! — c. young per.).

Chiloscyphus cordifolius Rodw. Pap. & Proc. Roy. Soc. Tasmania 1915:106. 1916 (seors. 31 December 1915) (see also vol. 2 of *Tasmanian Bryophyta*, p. 54. 1916), *syn. fide* Grolle (1966). Original material: Tasmania, Adamson's P., 1,100 m., December 1913, *Rodway* (hb. Grolle!, HO!).

Plants *soft, fleshy, the leaves and underleaves fragile, easily torn;* plants suberect, mixed with other bryophytes or in rather dense pure tufts, *whitish green to yellow-brown to brown;* axes to 8.5 cm. tall, *1.5 mm. wide, the apices usually swollen.*

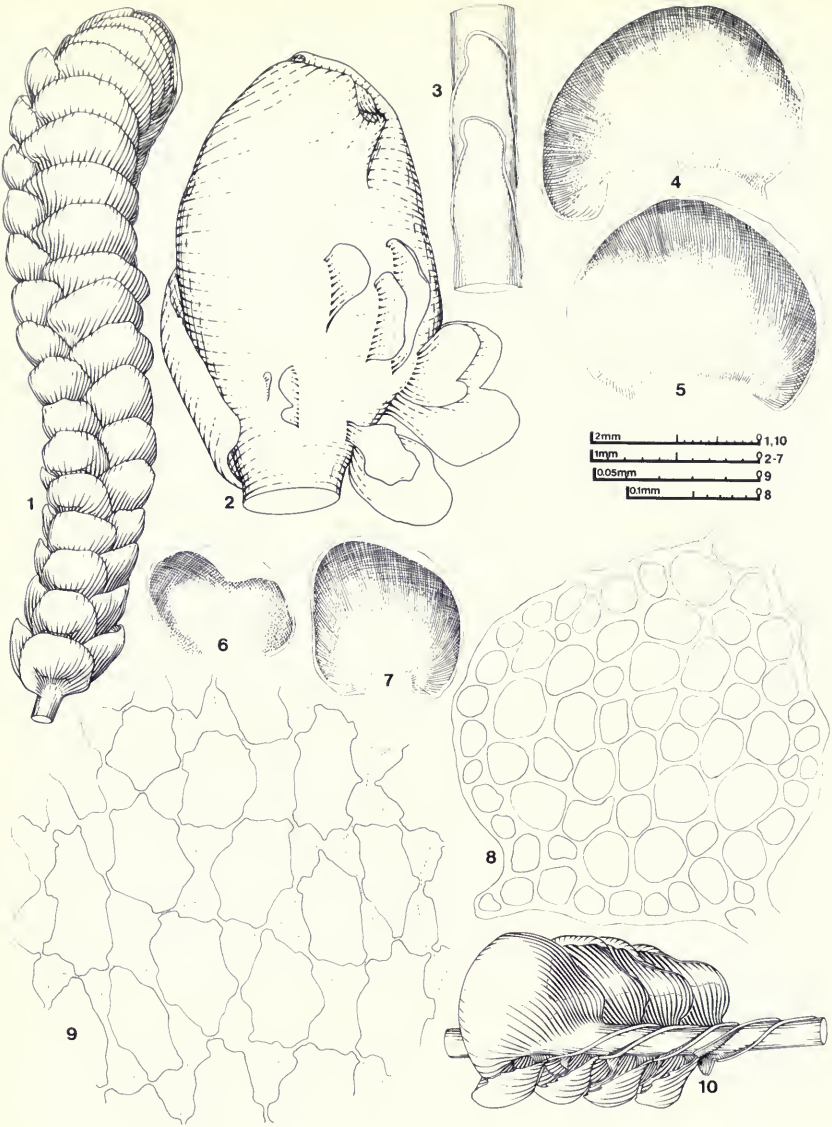


FIG. 55. *Clasmatocolea notophylla* (Hook. f. & Tayl.) Grolle. **1,** Portion of main axis, ventral-lateral view. **2,** Mature perianth showing scales (only the associated bracteole shown), dorsal-lateral view. **3,** Main axis, ventral view, showing underleaf and leaf insertion. **4, 5,** Leaves. **6-7,** Underleaves, dorsal view. **8,** Stem, cross section. **9,** Median leaf cells. **10,** Main axis, lateral view, leaves of one side and one underleaf removed. Figures 1, 4-9, from type of *C. notophylla*, *Hooker*, Auckland Is. (L); figure 2, from isotype of *Lophocolea tumida*, *Oldfield*, Tasmania (FH); figures 3, 10, from *Scott 1075*, Tasmania, Cradle Mt.

FIG. 56. *Clasmatocolea notophylla* (Hook. f. & Tayl.) Grolle.

Branches sporadic, of *lateral- and ventral-intercalary type*, the lateral-intercalary branches ventrally displaced, between ventral portion of leaf and edge of underleaf.

Stems 6-10 cells high, *cortex in a single row of moderately thick-walled cells smaller than the medullary cells*, the exposed wall of cortex very thickened; medullary cell walls moderately thickened; endophytic hyphae absent. Rhizoids in fascicles from stem near underleaf base.

Leaves with insertion slightly to distinctly recurved at ventral end; leaves usually connivent or nearly so dorsally, closely imbricate, conchiform concave, very broadly ovate to reniform, dorsal portion of leaf becoming moderately reflexed; apex broadly rounded, undivided, often slightly to distinctly inflexed, *the apex and margins entire*, although the margins sometimes with several slime papillae; *dorsal margin broadly rounded*, plane to sinuous, rather long decurrent; ventral margin inflexed, broadly rounded, *basal portion ± auriculate, extending ventrally beyond stem and in contact with spreading underleaf*, occasionally in contact with ventral margin of opposite leaf.

Leaf cells with massive, nodular or protuberant, irregularly triangular to rectangular trigones that are confluent or separated by narrow thin-walled places, the cell lumen bounded mostly by the massive trigones; median leaf cells 18-38(-42) μ wide, (23-)29-49(-53) μ long; cuticle smooth or roughened and then appearing finely granular.

Underleaves *3.1-3.6* $\times$ *stem width, connate on both sides with ventral-basal adaxial portion of leaf lamina or with ventral margin of leaf,* the attachment hidden by ventral-basal portion of leaves; underleaves moderately spreading, approximate to imbricate, *moderately to distinctly cupulate,* $\pm$ *orbicular to oblate,* basal portion abruptly convex (ventral view), and *often with a flange of tissue marginal to insertion; apex undivided and broadly rounded to truncate to broadly retuse,* the apices with 2 slime papillae or with (1-)2 teeth each terminating in a slime papilla; margins of the lamina with a few slime papillae and/or 1-4 few-celled teeth each terminating in a slime papilla.

Plants ?dioecious; androecia not seen. Gynoecia (only 2 mature gynoecia seen) on main axis; subfloral innovations from below bracteole of second series or absent; bracts in 3 series, those of innermost series deeply concave, with a deeply concave bulge in median-basal portion; apices undivided and broadly rounded, the apices and margins entire. Bracteole (of mature gynoecium) of innermost series *connate for ca. 0.3 its length on 1 side, short-connate on other side* or (in juvenile gynoecium) 0.3 connate with bracts on both sides, *deeply convex* (ventral view); lamina margins sparingly dentate. Perianth with *basal portion with numerous, large, irregular, commonly obovate, sometimes bilobed scales* attached to perianth for varying lengths, the scales occasionally attached to one another; perianth *subclavate,* $\pm$ *inflated and* $\pm$ *terete in basal portion,* the upper portion somewhat bilaterally compressed, expanding slightly toward mouth; perianth mouth $\pm$ bilaterally compressed due to infolded lobes, the lobes broadly rounded, incurved, entire. Seta present, but old, collapsed, and without a capsule.

Differentiation.—This species bears a superficial resemblance to some plants of the hygrophylous facies of *C. humilis. Clasmatocolea notophylla* may be distinguished by the following complex of characters: (a) leaf cells with massive, nodular or protuberant trigones that are confluent or separated by narrow thin-walled places; (b) leaves with dorsal margins rounded; (c) underleaves connate on both sides, and frequently with the ventral-basal adaxial portion of the leaf lamina; (d) underleaves consistently undivided; (e) bracteoles connate on both sides, and on one side (or both sides in one observed immature gynoecium) for ca. 0.3 its length; (f) basal portion of perianth with numerous large (some extending to ca. 0.5 perianth length) obovate scales that are attached to the perianth for varying lengths.[10] In view of the fact that characters listed in (a), (e), and (f) do not occur in any other *Clasmatocolea* taxon, *C. notophylla* stands quite isolated and should therefore not be confused with any other member of the genus.

Clasmatocolea notophylla shares some characters with *C. tjiwideiensis* of Java, which also has (a) deeply convex (ventral view) underleaves that are at least 3 $\times$ the stem width and sometimes undivided; (b) underleaves

[10] Unfortunately only two mature gynoecia were available for study. Characters (e) and (f) thus require verification with the study of more copious material.

at times connate on both sides, and on one side, at least, with the ventral-basal, adaxial portion of the leaf lamina; (c) the basal portion of the ventral margins of leaves extending ventrally beyond the stem. However, the highly unique characters of the gynoecium of *C. notophylla* isolate this species and negate any real, close relationship to *C. tjiwideiensis.*

Notes.—1. There has been considerable confusion regarding usage of the name *Clasmatocolea* "*Lophocolea*" *notophylla* in New Zealand. Some of the confusion can be traced to Hodgson (1953) and determinations by her. Hodgson's concept of "*Lophocolea*" *notophylla* can be explained by her statement (1953, p. 338), "Although there is no specimen of Taylor's type in either the Hooker or Mitten Herbarium, with which to compare the mainland plant, *Lophocolea okaritana* St., I believe that they are the same species. . . ." In Hodgson (1953) the description and all observed plants referred to by her as *Lophocolea notophylla* are actually *Lophocolea gunniana* Nees (with one exception: the specimen from Regina Valley, leg. *Teague* is *Clasmatocolea* cf. *vermicularis*). *Lophocolea okaritana* Steph. (Spec. Hep. 3:85. 1906, type: New Zealand, Okarito, *Kirk 592* G!), which is listed as a synonym of *C. notophylla* in Hamlin (1972), is a synonym of *Lophocolea gunniana* (*fide* Hamlin, 1973).

The confusion is compounded by Hodgson's (1953, p. 338) comment, "Judging by the drawing in Bastow's Plates of Tasmanian Hepatics, *Loph. austrigena* (Tayl.) Syn. Hep., of Tasmania, appears to be the same thing." This may explain why many of the collections of *Lophocolea gunniana* that I have studied are labeled *Lophocolea austrigena*, and further, several had originally been determined as *Lophocolea notophylla. Lophocolea gunniana* and *L. austrigena* (type—Cabo de Hornos, Chile) are actually very closely related, but based upon my studies to present, *L. austrigena* is restricted to Tristan da Cunha, Inaccessible I., the Falkland Is., and southern South America. Hodgson (1962) alludes to the error as she states for *Lophocolea austrigena* (p. 111), "Wrongly listed as *Lophocolea notophylla* (Hodgson, 1953)."

2. There seems to be confusion regarding pagination of several of the Rodway papers; the Rodway species I am citing here was published in the *Papers and Proceedings of the Royal Society of Tasmania.* The title page of the *article* bears the phrase "Issued separately (date)." *Chiloscyphus cordifolius* Rodw., for example, appears on p. 106 of the Papers and Proceedings for the year 1915 (*fascicle* issued 24 February 1916). The title page of the *article*, however, reads "Issued separately 31st December, 1915." The description was then republished in *Pap. & Proc. Roy. Soc. Tasmania* for the year 1916, the fascicle of which appeared on 19 February 1917. This Rodway paper was also issued, separately paged, on 30 August

1916, appearing as vol. 2 of *Tasmanian Bryophyta*. The latter has been widely distributed and is commonly cited.

Ecology.—In New Zealand in *Dacrydium* scrub (240 m.) or in *Sphagnum-Hypolaena-Dacrydium* bogs (at 915 m. and associated with *Anastrophyllum schismoides* and *Tetracymbaliella cymbalifera*) or on wet, peat-covered, south-facing ledges of cliff faces (sea level). In Tasmania it grows very loosely over ground or bryophyte-covered logs in *Nothofagus-Eucryphia*, *Nothofagus cunninghamii*, or *Nothofagus-Athrotaxis* forests (400-915 m.). It occasionally occurs over wet, peaty soil in subalpine seepage areas under protective cover of *Diselma archeri* (1,225 m.). In southern South America the species is restricted to the very wet, western fringe of the Patagonian Channels in Prov. Magallanes and Prov. Aisén. It occurs in pools and along streams in moorland areas and (rarely) on the floor of mossy forests.

Phytogeography.—Amphipacific temperate; Auckland Is.; New Zealand, South I.; Tasmania (400-1,225 m.); southern South America (Patagonian Channels N. to 48° 04′ S., Prov. Magallanes, Prov. Aisén) (see fig. 56).

Specimens seen.—**NEW ZEALAND. SOUTH ISLAND.** SOUTHLAND: Fiordland, Secretary I., ca. 240 m., *Baylis s.n.* as *Lophocolea austrigena* (CHR); ibid., *Baylis s.n.* — c. per. (hb. Grolle); Fiordland Natl. Park, Milford Sound, foot of Bowen Falls, *Schuster 55546b* (hb. Schuster). WESTLAND: Omoeroa R., S. of Franz Josef, towards Weheka Hills, *Schuster 67-241b* (hb. Schuster). WESTLAND/NELSON: Paparoa Range, 915 m., *Helms 244* as *Leioscyphus turgescens* (CHR). **TASMANIA:** Adamsons P. Track, *A. Ratkowsky 78/73* (F); near Manuka Flat on trail to Adamsons P., ca. 300-400 m., *Norris 26941* (F); plateau region E. and SE of Mt. Eliza summit, E. of L. Pedder, ca. 1,225 m., *Engel 13708* (F); upper reaches of S. facing slope of Sentinel Range, between Lakes Gordon and Pedder, 700 m., *Engel 15114* (F); L. Gordon, *Walters 79/17* (F); Mt. Arrowsmith, on Lyell Hwy., 2.7 mi. W. of King William Saddle, W. of Derwent Bridge, Surprise Valley, ca. 600 m., *Schuster 50372* (hb. Schuster); Cradle Mt.-L. St. Clair Natl. Park, Pine Valley, Cephissus Falls, NNW of L. St. Clair, 850 m., *Engel 14252* (F); Allans Cr., NE slope of Mt. Darwin, off Kelly Basin Road (Crotty Track), 410 m., *Engel 16529*, *16584* (F); Cradle Mt. Region, Cradle Mt., 915 m., *Scott 1075* (hb. Monash Univ.); Cradle Mt. Region, Dove L. Track, *A. Ratkowsky 79/16* (F); Cradle Mt. Region, Weindorfers Forest, along track from Waldheim Chalet to Hounslow Heath Track, 975 m., *Engel 14050* (F). **CHILE.** PROV. MAGALLANES: Pto. Alert, *Engel 5036*, *5061* (MSC). PROV. AISÉN: Pto. Island, *Engel 4268A* — c. young per., *4323A* (MSC).

Clasmatocolea verrucosa Engel. Figures 57, 58.

Clasmatocolea verrucosa Engel, Bryologist 83:220. *f. 1–19.* 1980. Holotype: Tasmania, E. slope of Black Bluff just below summit, S. of Burnie, 1,250 m., *Engel 15764* (F; isotype: HO).

Plants *soft, fleshy, the leaves and underleaves fragile, easily torn;* plants loosely creeping to suberect, in rather dense, pure tufts, yellow-brown, becoming brownish with age, highly nitid when dry; axes to 3 mm. wide.

Branches rather common, *mostly of* Frullania *type, occasionally of lateral-intercalary type,* the lateral-intercalary branches ventrally displaced, between ventral portion of leaf and edge of underleaf; ventral-intercalary branches very rare (only a few examples seen).

Stems narrow for plant size, 11-12 cells high, the cortex poorly differentiated, in a single row of slightly smaller cells; both the cortical and medullary cells moderately thick walled, but the exposed wall of cortex very thickened; *cuticle smooth.* Rhizoids in tight fascicles from stem near underleaf base, the rhizoids hyaline and often adhering to underleaf surface, the tips thick walled and often highly branched but nonseptate.

Leaves with insertion not or very slightly recurved at ventral end; leaves erect (but not connivent dorsally) to moderately spreading, moderately conchiform concave, broadly ovate to oblate; apex broadly rounded, undivided, *often sharply inflexed, lending a deeply concave, channeled appearance to that part of the leaf;* apex often repand, entire or with armature more sparing and smaller than that of margins; *dorsal and ventral margins armed with several irregular, often sharp teeth,* the margins sometimes with a small, accessory, armed lobe near the base; *dorsal margin straight or slightly rounded, undulate, sometimes reflexed;* ventral margin broadly rounded, but often straight near base.

Leaf cells with massive, coarse, irregularly triangular to rectangular trigones that are confluent or separated by narrow thin-walled places, the cell lumen bounded mostly by the massive trigones; median leaf cells 24-30(-36) μ wide, 31-41 μ long; *leaf cells on their inner and outer surfaces each with a large, domelike, prominent, hyaline verruca, the cells of the apex and margins of the leaves each with similar protuberances but with them peripherally extended beyond the outer cell wall.*

Underleaves *reniform, in width 2.2-2.9* $\times$ *their length* (when flattened) and *4.4-5.1* $\times$ *stem width, connate on both sides,* slightly spreading, *imbricate, distinctly concave* and with margins appressed to leaves; *apex undivided and broadly rounded to broadly retuse,* the apices with a few slime papillae along with a few teeth that commonly terminate in a slime papilla, the apices sometimes edentate; margins of the lamina sometimes inflexed, with a few slime papillae plus a few teeth and often laciniae, the armature commonly terminating in a slime papilla.

Plants dioecious; androecia intercalary on main axis or on rather long *Frullania-* or (occasionally) lateral-intercalary type branches; bracts with basal portion strongly saccate, the entire bract strongly concave, and with apices appressed to bract immediately above; lobule margin incurved to involute, broadly rounded, sparingly dentate-laciniate; antheridia solitary, the stalk uniseriate.

Gynoecia (only immature gynoecia seen) on main axes or innovations (plants sometimes repeatedly producing innovations each forming a perianth); subfloral innovations,

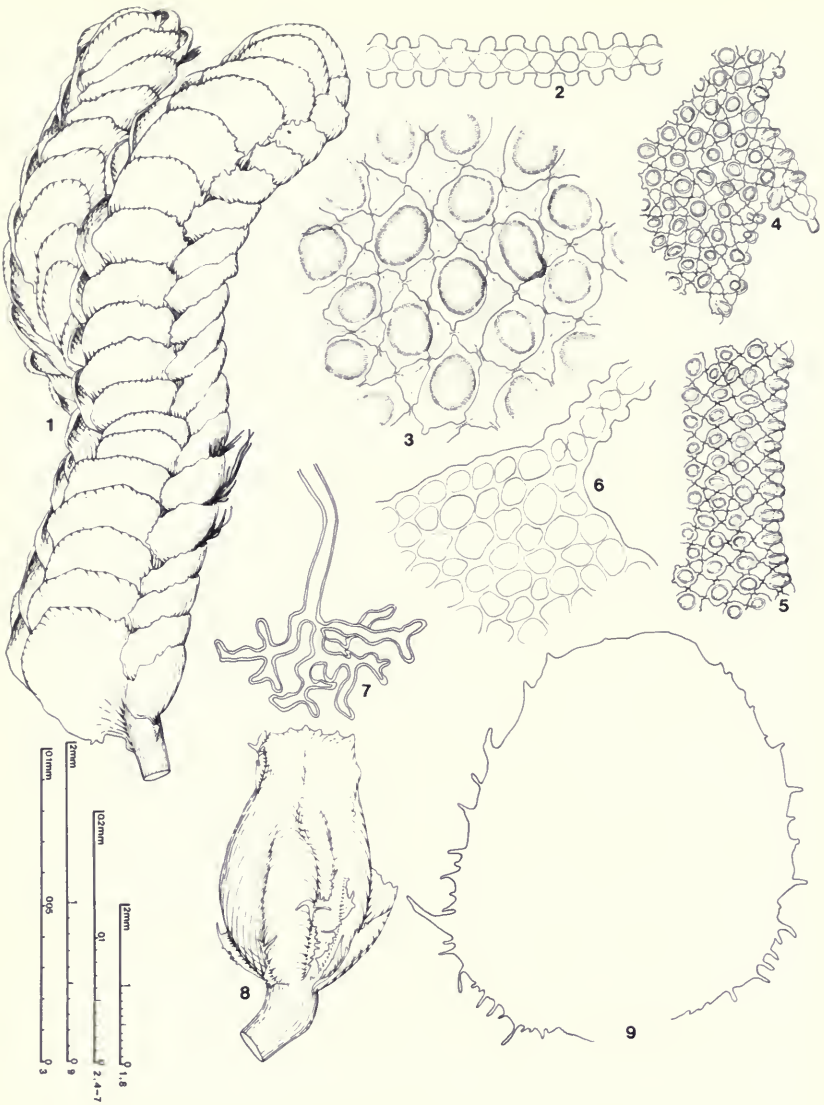


FIG. 57. *Clasmatocolea verrucosa* Engel. **1,** Leading axis with *Frullania*-type branch. **2,** Cross section through median portion of leaf. **3,** Median leaf cells showing cuticular verrucae. **4.** Cells of ventral margin of leaf. **5,** Cells of leaf apex. **6,** Stem with portion of leaf base, cross section. **7,** Rhizoid tip. **8,** Perianth showing scales, dorsal-lateral view (only the associated innermost bracteole shown). **9,** Bract of innermost series (not flattened). All from holotype.

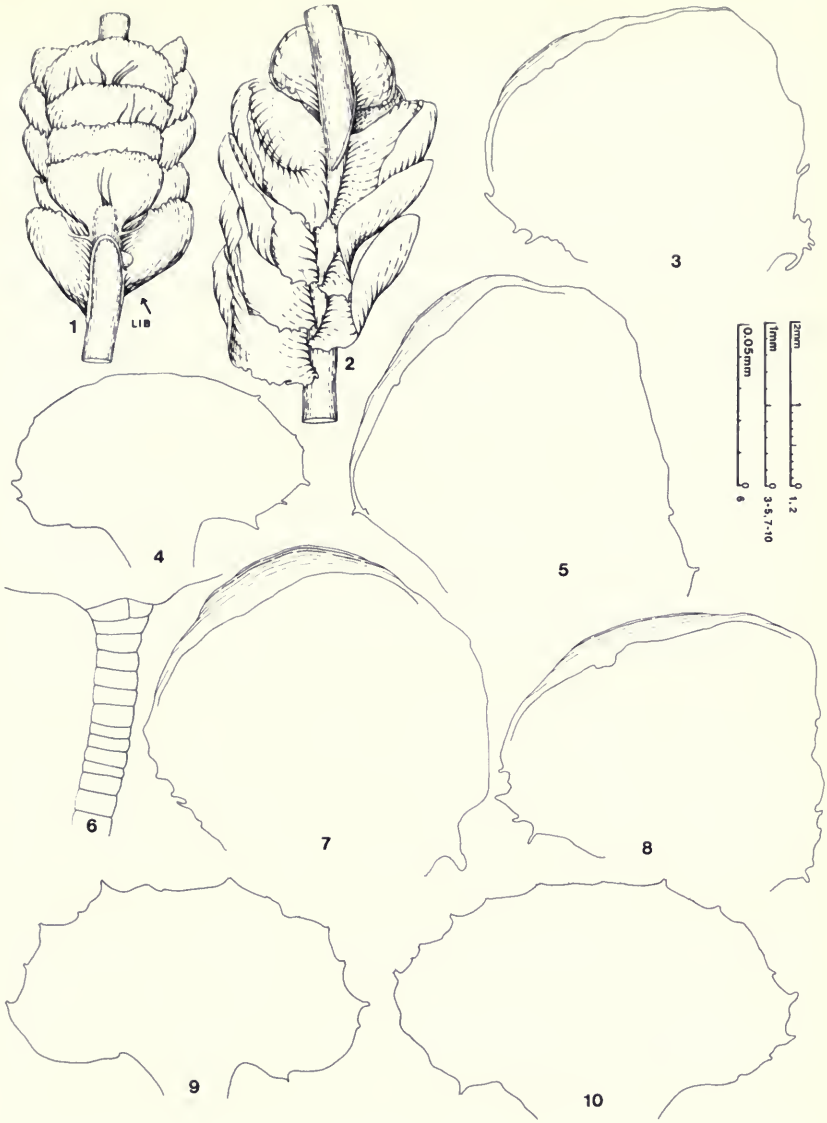


FIG. 58. *Clasmatocolea verrucosa* Engel. **1,** Portion of main axis, ventral view (LIB = lateral-intercalary branch). **2,** Portion of main axis, dorsal view. **3, 5, 7, 8,** Leaves of main axis (not flattened). **4, 9, 10,** Underleaves of main axis (flattened). **6,** Antheridial stalk. All from holotype.

when present, from below bract or bracteole of innermost or second series; bracts in 3 series, those of innermost series often closely appressed to perianth, the bracts rather deeply concave, with a deep, vertically elongate, concave bulge in median-basal or dorsal-basal portion; apex undivided, broadly rounded, irregularly dentate; lamina margins rather abundantly and sharply dentate-laciniate. Bracteoles of innermost series free or short connate on 1 side, rather convex (ventral view); apex undivided, with several irregular, small teeth; lamina margins with several sharp teeth. Perianth with *basal portion with several large, vertical, irregular, ciliate to laciniate scales or lamellae* attached to perianth for varying lengths; perianth *broad and stoutly ovate, inflated and weakly trigonous in the basal portion* (the angles blunt and broadly rounded), the upper portion somewhat bilaterally compressed, slightly narrowing toward mouth; perianth lobes broadly rounded, armed with several irregular, often sharp teeth, the ventral lobe somewhat smaller and more narrowly rounded, the ventral lobe somewhat longitudinally folded, rendering the perianth distally bilaterally compressed; perianth cells with papillae similar to those of the leaves.

Sporophyte not seen.

Differentiation.—The manuscript of this paper was originally completed and submitted with *C. notophylla* treated as an isolated taxon and placed in its own subgenus. While subsequently working on my Tasmanian collections, I became aware of the remarkable *C. verrucosa*, which, in all cases, was mistaken for *C. notophylla* in the field. This field misidentification is not surprising, for the two taxa have a similar facies and share the following features: (a) plant size, although *C. verrucosa* is a bit larger; (b) leaf shape, with apices undivided and broadly rounded; (c) leaf cells with massive, coarse trigones that are confluent or separated by narrow thin-walled places; (d) underleaves connate with leaves on both sides; (e) underleaves large, deeply concave, and with apices undivided and broadly rounded to broadly retuse; and (f) perianth with scales of varying sizes. However, *C. verrucosa* may be immediately distinguished by (a) the huge cuticular verrucae, one each per cell; (b) the predominance of *Frullania*-type branching; (c) the armature of the dorsal and ventral margins of the leaf; (d) the straight or at most slightly rounded dorsal margin of the leaf; (e) the reniform underleaves that are 2.2-2.9 × wider than high and 4.4-5.1 × the stem width; and (f) the armed perianth scales and dentate perianth lobes.

The only other members of the genus with cuticular excrescences are the unrelated *C. strongylophylla* and *C. tjiwideiensis* (both Subg. *Clasmatocolea*), both of which have a papillose cuticle.

Note.—With the use of depth focusing, the cuticular verrucae may be observed, one each per cell, oriented directly above the cell lumen and *not* over the cell wall. This is the case in all leaf cells except those of the marginal row. The marginal row has cuticular protuberances similar to those of the interior cells, but differs in having the verrucae peripherally

extended beyond the outer cell wall. This feature lends a definite warty appearance to the leaf, which is useful in identifying the plants. The verrucae may be readily observed in profile on the leaf apices and margins, utilizing the dissecting microscope.

Ecology-Phytogeography.—This subalpine-alpine species, found between 1,000-1,300 m., is endemic to Tasmania. It typically grows along creek banks or pool margins, as well as under protective cover of rock ledges or shrubs. One collection (*Norris 27866*) occurred in the upper limits of a *Nothofagus* forest.

Specimens seen.—**TASMANIA:** Mt. Field Natl. Park, Mt. Mawson Plateau, above and W. of L. Dobson and S. of L. Seal, 1,250 m., *Engel 13089, 14327* (F); Mt. Field Natl. Park, Rodway Range, between Rodway Ski Tow and K Col area, 1,240-1,310 m., *Engel 14416* — c. ♂ (F); W. side of Mt. Eliza, 800-1,200 m., *Norris 31007* (F); L. St. Clair Region, trail from L. Solitude to Little Hugel, 1,000-1,100 m., *Norris 27866* (F); Cradle Mt.-L. St. Clair Natl. Park, The Labyrinth, NNW of L. St. Clair, 1,130 m., *Engel 14272A* (F); Cradle Mt. Region, Plateau Cr. area, between Cradle Plateau and Marions Lookout, 1,250 m., *Engel 13966, 13979* — c. young per. (F); E. slope of Black Bluff just below summit, S. of Burnie, 1,250 m., *Engel 15764* — c. per. (F).

Subg. **PLICATICALYX** Engel, subg. nov.

Folia caulina indivisa, parce dentata; amphigastria caulina cucullata, basi auriculata, habentia unum lobum basale parte extensum ultra caulis dorsalem paginam; androecia latiora quam sterile parte axis; ♂ bracteae lobuli 1-3-laciniati ad lobati; perianthia valde ovoidea, apice 4-5-plicato, ore contracto, lobi copiose dentati ad laciniatos; sporae 24-27(-30) μ, cum anguste conicis prominentiis.

Type species: *Clasmatocolea cucullistipula* (Steph.) Grolle.

Leaves undivided, sparingly dentate; underleaves cucullate, auriculate at base, with one lobe in basal portion of underleaf which extends beyond dorsal surface of stem; androecia wider than sterile parts of axis; ♂ bract lobules 1-3-laciniate to lobate; perianth stoutly ovoid, apex 4-5-plicate, the mouth contracted, the lobes copiously dentate to laciniate; spores 24-27(-30) μ, the exine with narrowly conical projections.

Distribution.—Southern South America.

Clasmatocolea cucullistipula (Steph.) Grolle. Figures 59-61, Plates 28, 29.

Lophocolea cucullistipula Steph. Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26 (III, 6):37. 1900. *Clasmatocolea cucullistipula* (Steph.) Grolle, Rev. Bryol. Lichénol. 29:71. 1960. Lectotype (*nov.*): Chile, Prov. Chiloé, I. Guaitecas, (Melinca), April 1896, *Dusén 376*, ex hb. Dusén (S!).

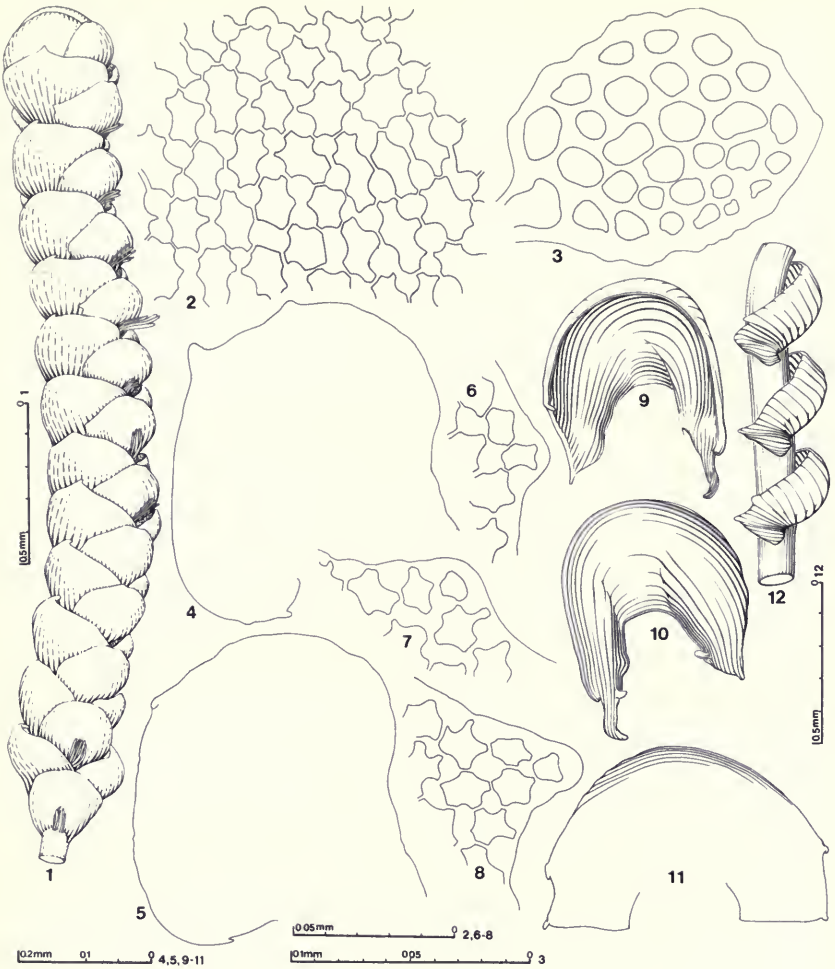


FIG. 59. *Clasmatocolea cucullistipula* (Steph.) Grolle. **1,** Main axis, ventral-lateral view. **2,** Median leaf cells. **3,** Stem, cross section. **4, 5,** Leaves (flattened). **6-8,** Teeth of leaf apex. **9,** Underleaf, dorsal view. **10,** Underleaf, ventral view. **11,** Underleaf (nearly flattened). **12,** Axis with leaves removed, lateral view. All from lectotype of *L. cucullistipula*, *Dusén 376*, Chile, Prov. Chiloé, I. Guaitecas.

FIG. 60. *Clasmatocolea cucullistipula* (Steph.) Grolle. **1,** Axis with perianth. **2, 3,** Portions of perianth mouth. **4, 5,** Perianth, cross section through portion just below apex. **6,** Perianth, cross section through median portion. **7,** Portion of perianth mouth. **8,** Androecial axis (note width compared to sterile portions). **9, 10,** Male bracts showing lobule armature. **11,** Capsule wall, cross section. **12,** Outer capsule wall cells. **13,** Inner capsule wall cells showing portion with semiannular bands sparsely developed. **14,** Seta, cross section. Figures 1-4, 6,7, from *Engel 4496*, Chile, Prov. Magallanes, I. Williams; figure 5, from *Engel 4293*, Chile, Prov. Aisén, Pto. Island; figures 8-10, from *Engel 5543*, Chile, Prov. Magallanes, Pto. Bueno; figures 11-14, from syntype of *L. cucullistipula*, *Dusén s.n.*, Chile, Prov. Chiloé, I. Guaitecas.

Lophocolea filiformis Steph. Bull. Herb. Boissier 6:661. 1906 (= Spec. Hep. 3:77), *syn. nov.* Holotype: Chile, Prov. Valdivia, Valdivia, *Hahn*, ex hb. Jack (G!).

Lophocolea cucullifolia Steph. Spec. Hep. 6:269. 1922, *syn. nov.* Holotype: Chile, Prov. Chiloé, I. Chiloé, *sin. coll.*, ex hb. Jack (G! — c. per.).

Plants prostrate or suberect, or subpendent, in loose or dense, *usually pure tufts, pale olive green-light brown to pale brown, nitid when dry, capillaceus, obscurely to distinctly moniliform* (especially in ventral-lateral view); *axes 350-490 μ wide*, the leaves and underleaves fragile, easily tearing.

Branches rather common, Frullania-*type predominating, ventral-intercalary type occasional, lateral-intercalary type absent.*

Stems (5-)6 cells high, cortex in 1 row of *very thick-walled cells* the same size as or slightly smaller than the medullary cells, the exposed wall very thickened; *medullary cell walls very thickened;* endophytic hyphae in both cortex and medulla or absent. *Rhizoids in very tight fascicles from a region that includes both the stem immediately at underleaf base and the median basal portion of an underleaf*, the rhizoids often tearing off with underleaf.

Leaves with insertion distinctly recurved at ventral end; leaves strongly erect (axis commonly appearing channeled in dorsal view), occasionally connivent, loosely imbricate, conchiform concave, ± *oblate to broadly ovate;* apex broadly rounded to ± truncate, undivided, *with 1 or a few small teeth;* dorsal margin ± straight in proximal half, *entire or with 1 or a few small teeth*, short decurrent; ventral margin broadly rounded, *entire or with 1 or a few small teeth, the basal portion subauriculate, extending across stem and nearly in contact with or occasionally overlapping ventral margin of opposite leaf.*

Leaf cells thin walled, trigones massive, coarse and nodular, often confluent, commonly with leaf cell lumen, except for the narrow thin-walled places, bounded mostly by the massive trigones; median leaf cells 11-18(-22) μ wide, 13-24 μ long; cuticle smooth or slightly roughened and appearing finely granular.

Underleaves 2.4-5 × stem width, free, apical portion appressed to stem or ventral margin of leaf, the underleaves approximate, *cucullate*, ± *clasping stem, the margins curved dorsally and very often extending above dorsal stem surface, auriculate at the base; apices undivided, broadly rounded*, occasionally retuse, occasionally with 2 slime papillae or 1-celled teeth terminating in slime papillae; margins in *basal portion with 1 lobe that extends above dorsal stem surface*, the lobe terminating in a slime papilla, the margins in median portion with a slime papilla or a tooth terminating in a slime papilla.

Plants dioecious; androecia intercalary on main axis or long *Frullania*-type branches, *wider than sterile portions of axis*, densely imbricate, *leaving a narrow strip of exposed stem tissue;* bracts with basal portion strongly saccate, distal portion strongly concave, with apices appressed to bract immediately above, the apices with a few teeth; *lobule margin with 1-3 erect or involute laciniae or small lobes* that may or may not terminate in a slime papilla; antheridia solitary, stalk uniseriate.

Gynoecia on main axis or long *Frullania*-type branches or ventral-intercalary subfloral innovations, often copiously produced; subfloral innovations originating from

below bracteoles of first or second series or absent; bracts in 3-4 series, those of innermost series deeply concave to subnavicularifform to wide-elliptic to wide-ovate; apices broadly rounded, *with several teeth and laciniae or lobes*, the laciniae and lobes sometimes dentate; *lamina margins with a few to several laciniae and rounded or sharp lobes and a few teeth.* Bracteoles of innermost series ca. equal to bract size, free from bracts, deeply convex (ventral view), ovate; apices rounded, *with several small teeth and sometimes laciniae; lamina margins with a few to several irregularly shaped laciniae, rounded or sharp lobes, a few teeth*, and a few slime papillae, the armature occasionally rather copious. *Perianth subterete-obscurely to moderately trigonous, slenderly to rather stoutly ovoid, rather strongly inflated in median and basal portions, the apex 4-5-plicate*, the ventral side strongly convex throughout, to moderately infolded throughout, or sometimes infolded in apical and median portions with the basal portion convex; *perianth sides gradually or abruptly narrowing toward the rather contracted mouth;* lobes very broadly rounded, *copiously dentate to laciniate, the laciniae commonly narrow and dentate.*

Seta 5 cells in diameter, with 14 rows of outer cells surrounding an inner core of scattered cells that are ca. equal to outer row, the core cells with corners thickened similarly to small trigones. Capsule valves 0.59-0.77 mm. long, 38-46 μ thick, of (4-)5 layers. the outer row of cells equal to thickness of 2.2-2.8 of interior strata; outer layer with red-brown, nodule-like or wide spinelike thickenings that are often moderately tangentially dilated, semiannular bands very common; exposed wall moderately thickened; intermediate and inner layers subequal in thickness or inner layer slightly less thick, the intermediate layers with thickenings often considerably tangentially dilated, semiannular bands occasionally present; inner layer of cells with red-brown semiannular bands sporadic to rather common, the radial walls with nodulose thickenings very common.

Spores 24-27(-30) μ, light brown, *exine with* $\pm$ *hyaline, narrowly conical, rather dense projections* with radiating bases *and dilated tips, the tips with finger-like projections that are erect, laterally extended or recurved; spores averaging 2.8* $\times$ *elater diameter.* Elaters 8-10 μ wide, spiraled to tips, elater walls red-brown.

Differentiation.—This well-defined species, which exhibits comparatively little variability, should offer no confusion with any other member of the genus. If sterile plants of *C. cucullistipula* are at hand, the following ensemble of features will serve to identify it: (a) the cucullate, free, undivided underleaves that are auriculate at the base and that have a conspicuous lobe in the basal portion extending dorsally beyond the dorsal surface of the stem; (b) the 1-4-dentate leaf margins; (c) the distinctive branching pattern, with *Frullania* type in predominance, ventral-intercalary type occasional and *lateral-intercalary type absent;* (d) the small axis size (350-490 μ wide); (e) the characteristic stems that are (5-)6 cells high and that have both the poorly differentiated cortex and the medulla of very thick-walled cells; (f) the large and bulging leaf cell trigones; (g) the distinctive and characteristic habit of loosely to densely intertwined, nearly pure tufts loosely adhering or semipendent from very small branches or twigs (this habit alone will distinguish *C. cucullistipula* from all other American taxa); and (h) the light olive green-light brown color. If an-

FIG. 61. *Clasmatocolea cucullistipula* (Steph.) Grolle.

droecia are present, the unique combination of the androecia being wider than sterile portions of an axis and the frequently 2-3-laciniate to lobate bracts will further serve to distinguish the taxa. Perianths will provide the following additional ensemble of distinctive features: (a) the slenderly to rather stoutly ovoid shape; (b) the obscurely to moderately trigonous basal and median portions; (c) the 4-5-plicate apical portion with the contracted mouth; and (d) the copiously dentate and laciniate lobes. Further, the spores are 24-27(-30) μ and larger than those of any other member of the genus. The spore wall is also unique.

The above combination of characters, taken collectively, support an isolated position of the species within the genus. Indeed, with the number of unique features one could, with certain justification, argue for removal of the species from *Clasmatocolea* and for creation of a new, monotypic genus for it. However, I believe its natural affinities are with *Clasmatocolea*, where I choose to retain it.

The species has some relationship with Sect. *Strongylophyllae*—on the one hand there is the branching pattern, stem anatomy, relatively small axis size, and large to bulging trigones of *C. strongylophylla*, whereas on the other hand, the cucullate underleaves and dentate leaves remind one of *C. tjiwideiensis*. However, I believe the species is most closely allied with Sect. *Clasmatocolea*.

Note.—The syntypes of *Lophocolea cucullistipula* from the Río Aisén Valley are misdeterminations of *Xenocephalozia navicularis*. Of the remainder of syntypes, all from Islas Guaitecas, *Dusén 376* (S) best fits the original description and is here designated the lectotype.

Ecology.—Corticolous; mostly on small branches and larger twigs of shrubs such as *Pernettya* or *Berberis illicifolia* or of trees such as *Nothofagus*, *Saxegothaea*, or *Fitzroya*. When on twigs and small branches, the species nearly always occurs in pure tufts, because this is one of the few bryophytes of this region that has taken advantage of this kind of niche. When on tree trunks, however, it not uncommonly is intermixed with other hepatics such as *Frullania* spp., *Clasmatocolea gayana*, *Porella subsquarrosa*, *Lepicolea ochroleuca*, *Metzgeria* sp., and *Plagiochila* sp. Less commonly on bark of tree trunks. Ranging in altitude from near sea level in Prov. Magallanes to 1,000 m. (Cordillera Pelada) in Prov. Valdivia.

Phytogeography.—Patagonian Channels (not S. of ca. 51° S. in Prov. Magallanes) and in Valdivian region N. to 39° 16′ S. (Prov. Cautín) (see fig. 61).

Specimens seen.—**CHILE.** PROV. MAGALLANES: Head of Pto. Bueno, *Engel 5543* — c. per. + ♂ (MSC); I. Chatham, N. shore of B.

Wide, *Engel 5368C* — c. per. (MSC); E. side of I. Juan, *Engel 5286* — c. per. (MSC); Pto. Alert, *Engel 5033* — c. ♂ (MSC); SE point of I. Williams, *Engel 4488* — c. ♂, *4496* — c. per. (MSC). PROV. AISÉN: Pto. Island, *Engel 4293* — c. sporo. (MSC); Pen. de Taitao, B. San Rafael, *Gusinde s.n.* (JE); R. Aisén, *Dusén s.n.* as syntype of *L. cucullistipula* (NY); ibid., *Dusén 538* as syntype of *L. homomalla* (G); I. Magdalena, *Schwabe 33a* as *L. filiformis* — c. ♂ (JE); ibid., 6 m., *Schwabe 33/b* as *C. fulvella* — c. per. (hb. Grolle); Pto. Puyuhuapi, *Schwabe 4/b* (JE); ibid., *Schwabe 9/f-7/f* as *C. fulvella* (hb. Grolle); ibid., *Schwabe 23/b p.p.* as *L. navistipula* (JE); ibid., *Schwabe 50/b* (JE); ibid., R. Obscuro, *Schwabe 21/a* — c. ♂ (hb. Grolle); ibid., *Schwabe 21/b* as *C. fulvella* — c. per. (JE). PROV. CHILOÉ: I. Guaitecas, *Dusén s.n.* as syntype of *L. cucullistipula* (G — c. ♂, LD — c. per., NY, O — c. per.); ibid., *Dusén 343* as syntype of *L. cucullistipula* (FH, O); ibid., *Halle s.n.* — c. per. (G); ibid., Bo. Chica, *Dusén 367* (NY); I. Chiloé, 1.3 km. by road N. of junction of Ruta 5 and road to Delcahue, ca. 100 m., *Engel 12175* (F); I. Chiloé, Aguas Buenas area, 4.7 km. E. along Aguas Buenas road from Ancud-Quemchi road, ca. 100 m., *Engel 12215* — c. per. (F). PROV. LLANQUIHUE: L. Todos los Santos, Cayutué, *Wolffhügel s.n.* as *L. cucullifolia* (JE, S). PROV. OSORNO: Refugio Antillanca, 1,160 m., *Engel 3903* (MSC); around L. Toro on road to Refugio Antillanca, 855 m., *Engel 3999* (MSC). PROV. VALDIVIA: E. slope of Cord. Pelada, E. of El Mirador, between La Union and Pta. Hueicolla, 740 m., *Engel 12478* (F); Cord. Pelada, summit of El Mirador, between La Union and Pta. Hueicolla, 1,000 m., *Engel 12398* (F); W. slope of Cord. Pelada, W. of El Mirador, between La Union and Pta. Hueicolla, 680 m., *Engel 12331* — c. per. (F); Corral [Quitaluto], *Hosseus 114, 613 ex p., 643, 657 ex p., 668A* (JE); ibid., *Krause s.n.* as *Jungermannia moniliformis* Ångstr., **nom. hb.** (hb. Váňa); C. Lungoico, *Schwabe s.n.* (hb. Grolle). PROV. CAUTÍN: Villarica, *Ruthsatz s.n.* (JE). Patagonia: (All *sin. loc.* and all probable syntypes of *L. cucullistipula*), *Dusén 304* (G), *Dusén 343* (FH, G), *Dusén 367* — c. ♂ (G); (*sin. loc.*, probable syntype of *L. homomalla*), *Dusén 376* (FH, G).

XI. EXCLUDENDA

1. **Clasmatocolea abnormis** (Besch. & Mass.) Grolle.

Leioscyphus (?) *abnormis* Besch. & Mass. Bull. Mens. Soc. Linn. Paris 1:629. 1886. *Lophocolea abnormis* (Besch. & Mass.) Steph. Spec. Hep. 3:62. 1906. *Clasmatocolea abnormis* (Besch. & Mass.) Grolle, Rev. Bryol. Lichénol. 29:71. 1960. *Stolonophora abnormis* (Besch. & Mass.) Engel & Schust. Fieldiana, Bot. 36:114. 1975. *Hepatostolonophora abnormis* (Besch. & Mass.) Engel & Schust. *in* Engel, J. Hattori

Bot. Lab. 46:94. 1979. Type: Chile, Prov. Magallanes, I. Hoste, *Hyades* (FH!, G!, hb. Grolle!) (c. per.).

Jamesoniella gracilis Gola, Nuovo Giorn. Bot. Ital. II. 29:164. 1923, *syn. fide* Engel (1978). Original material: Chile, Prov. Magallanes, B. Ainsworth, (Ghiacciaio), 27 February 1913, *De Gasperi s.n.* (FI!). (Lophocoleaceae).

This species belongs in *Hepatostolonophora;* see Engel & Schuster (1975) and Engel (1979b).

2. **Clasmatocolea acutiloba** Schiffn.

Clasmatocolea acutiloba Schiffn. *in* Schiffner & S. Arnell, Österr. Akad. Wiss., Math.-Naturwiss. Kl., Denkschr. 111:63. *pl. 10, f. 112 a-g.* 1964 ≡ **Cylindrocolea acutiloba (Schiffn.) Engel, comb. nov.** Holotype: Brazil, Estado de São Paulo, "prope Lapa ad flumen Tiefé juxta São Paulo," 800 m., *Schiffner 2259* (W!). (Cephaloziellaceae).

This species appears to be an ally of *Cylindrocolea rhizantha* (Mont.) Schust.

3. **Clasmatocolea cuneifolia** (Hook.) Spruce.

Jungermannia cuneifolia Hook. Brit. Jungerm. *pl. 64.* 1814. *Mylius cuneifolius* (Hook.) S. Gray, Nat. Arr. Brit. Pl. 1:694. 1821. *Aplozia cuneifolia* (Hook.) Dum. Bull. Soc. Roy. Bot. Belgique 13:55. 1874. *Coleochila cuneifolia* (Hook.) Dum. Bull. Soc. Roy. Bot. Belgique 13:106. 1874. *Clasmatocolea cuneifolia* (Hook.) Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15:440. 1885. *Leptoscyphus cuneifolius* (Hook.) Mitt. Hooker's J. Bot. Kew Gard. Misc. 3:358. 1851. *Leioscyphus cuneifolius* (Hook.) Steph. Bull. Herb. Boissier 6 (3):218. 1906 (= Spec. Hep. 3:18). *Anomylia cuneifolia* (Hook.) Schust. Amer. Midl. Naturalist 62:53. 1959. Original material: Ireland, Bantry, *Hutchins* (*non vidi*). (Lophocoleaceae).

See Grolle (1962) for taxonomic treatment and illustrations and Grolle (1956, p. 294).

4. **Clasmatocolea doellingeri** (Nees) Steph.

Jungermannia doellingeri Nees *in* G. L. & N. Syn. Hep. 104. 1844. *Clasmatocolea doellingeri* (Nees) Steph. Bull. Herb. Boissier 6 (5):391. 1906 (= Spec. Hep. 3:48 [sic, *in errore pro* 47]). *Chonecolea doellingeri* (Nees) Grolle, Rev. Bryol. Lichénol. 25:295. 1956. Original material: "In Brasilia, super truncos, in caespite *Octoblephari albidi* (Hb. N. ex Hb. Doellinger.). Vidi etiam in Herb. Hampeano, a Siewers e Brasilia adlata specimina." (*non vidi*). (Chonecoleaceae).

See Grolle (1956) and Schuster (1958) for taxonomic treatments, including illustrations, and Grolle (1960, p. 87) for discussion of taxonomy and type.

Specimens seen.—**ARGENTINA.** PROV. BUENOS AIRES: Sa. de la Ventana, 540 m., *Roivainen 369b* (F, H). **BRAZIL.** San Cristobol, *sin. coll.* — c. sporo. (M). ESTADO DE SÃO PAULO: Município de São Paulo, Instituto de Botânica, *Vital 1283* (F, SP); Município de Itirapina, *Vital 117*, *136*, *2060* (F, SP); Município de Pirassununga, *Vital 1754* (F, SP); Município de Rancharia, *Vital 2577* (F, SP). **UNITED STATES.** FLORIDA: Sanford, *Rapp s.n.* (F, L, M — c. sporo., TENN); Marion Co., Ocala Natl. Forest, Juniper Springs, *Schuster 31520* (TENN).

5. **Clasmatocolea exigua** Steph.

Clasmatocolea exigua Steph. Bull. Herb. Boissier 6 (5):391. 1906 [= Spec. Hep. 3:48 (sic, *in errore pro* 47)]. Original material: North America, Louisiana, *Langlois* (FH!) = *Cylindrocolea rhizantha* (Mont.) Schust. Nova Hedwigia 22:175. 1972 (1971), *syn. fide* Fulford (1976). (Cephaloziellaceae).

See Grolle (1956, p. 298) and Schuster (1958).

6. **Clasmatocolea fiordlandiae** (Hodgs.) Grolle.

Clasmatocolea fiordlandiae (Hodgs.) Grolle, Rev. Bryol. Lichénol. 29:72. 1960 ≡ *Lophocolea fiordlandiae* Hodgs. Trans. Roy. Soc. New Zealand 80:340. *f. 15.* 1953. Original material: New Zealand, South Island, Fiordland, Caswell Sound, 27 March 1949, *Zotov 5235* (CHR! — c. ♂; hb. Grolle!). (Lophocoleaceae).

I believe the rightful place of this species is in the genus *Lophocolea*, because the leaves are plane and not adaxially concave. The leaves, however, sometimes have apices that are inflexed so that the leaves, then, appear concave in the *distal* portions. Further, the species is more closely related to taxa in *Lophocolea* rather than to any taxon assigned to *Clasmatocolea*.

Calyptrocolea perssonii Schust. was erroneously placed in the synonymy of "*Clasmatocolea*" *fiordlandiae* by Grolle (1972a). See Engel (1979b) where the name is in varietal rank—*Hepatostolonophora rotata* var. *perssonii* (Schust.) Engel; see also Engel & Schuster (1975).

7. **Clasmatocolea fragillima** Spruce.

Clasmatocolea fragillima Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15:440. 1885. Original material: Ecuador, M. Tunguragua, *Spruce* (*non vidi*) = *Leptoscyphus liebmanianus* (Lindenb. & Gott.) Mitt.

Hooker's J. Bot. Kew Gard. Misc. 3:358. 1851, *syn. fide* Grolle (1960). (Lophocoleaceae).

See Grolle (1960, p. 86) and Fulford (1976, p. 511), who synonymizes the species with *Leptoscyphus porphyrius* (Nees) Grolle.

8. **Clasmatocolea georgiensis** (Gott.) Grolle.

Lophocolea georgiensis Gott. Ergebn. Deutsch. Polar-Exped. 2 (16):453. *pl. 3-4*. 1890. *Clasmatocolea georgiensis* (Gott.) Grolle, Brit. Antarc. Surv. Bull. 28:86. 1972. *Evansianthus georgiensis* (Gott.) Schust. & Engel, Bryologist 76:518. 1973. Lectotype (*fide* Grolle, 1972b): South Georgia, 10 May 1883, *Will 11* (M!). (Lophocoleaceae).

For treatment of this species, including illustrations, see Schuster & Engel (1973).

9. **Clasmatocolea innovata** Herz.

Clasmatocolea innovata Herz. *in* Herzog & Noguchi, J. Hattori Bot. Lab. 14:39. *f. 7 a-g*. 1955 ≡ *Phragmatocolea innovata* (Herz.) Grolle, Rev. Bryol. Lichénol. 25:299. 1956. Holotype: Taiwan, Karobetsu, 100 m., *Schwabe 20* (*non vidi*). (? Jungermanniaceae).

Grolle (1956), who provides illustrations and a discussion of the taxonomy of the species, places the taxon provisionally in the Jungermanniaceae (*s. str.*). However, Schuster (1958, p. 16) and Váňa (1975, p. 365) express reservations regarding this placement.

10. **Clasmatocolea navicularis** (Steph.) Grolle.

Lophocolea navicularis Steph. Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26 (III, 6):43. 1900. *Clasmatocolea navicularis* (Steph.) Grolle, Rev. Bryol. Lichénol. 29:72. 1960. *Xenocephalozia navicularis* (Steph.) Schust. Nova Hedwigia 10:25. 1965. Lectotype (*fide* Grolle, 1966): Chile, Prov. Aisén, R. Aisén Valley, *Dusén* (*non vidi*).

Jungermannia chilensis Mont. Ann. Sci. Nat. Bot. III. 4:349. 1845 *non J. chilensis* Lehm. Nov. Minus Cogn. Stir. Pug. 6:36. 1834 (= *Porella*), *syn. fide* Grolle (1966). *Microlejeunea chilensis* (Mont.) Steph. Spec. Hep. 5:835. 1915. Original material: Chile, (Prov. Chiloé), without specific locality, *Gay* (BM!, G!).

Drepanolejeunea stephaniana Mass. Atti Accad. Sci. Med. Nat. Ferrara 80:9. *f. 1-4*. 1906, *syn. fide* Grolle (1966). Original material: Patagonia, Poyo-huapi, *Spegazzini* (*non vidi*).

Cephalozia trisetosa Steph. Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26 (III, 6):48. 1900, *nom. nud. pro syn.* (Lophocoleaceae).

Differentiation.—The nearest relative of *X. navicularis* appears to be the at least occasionally corticolous *Clasmatocolea trachyopa*, which also has (a) distinctly divided leaves, with the ventral portion incurved and flattened parallel to the ventral stem surface, lending a pouchlike concavity in the ventral portion of the leaf; and (b) strongly trigonous perianths with bifid lobes. *Clasmatocolea trachyopa* is distinct by the strongly oblique, often highly complex and ornamented leaves, with the insertion broad. *Xenocephalozia*, on the other hand, has transverse to weakly incubously inserted, entire or sparingly armed leaves with the insertion narrow. It is of interest, however, to note that depauperate axes of *C. trachyopa* not only have subtransversely inserted leaves with a narrow insertion, but lack some of the intricate ornamentation typical of well-developed facies of the species; these plants look strikingly like the spinose-leafed facies of *Xenocephalozia.*

Schuster (1965a, 1965b) thought *Xenocephalozia* belonged near *Clasmatocolea*, although in the latter paper he emphasized the isolation of *Xenocephalozia.* Grolle (1966) regarded the plant as a *Clasmatocolea*, but thought the species unique enough to place it in its own subgenus—Subg. *Schusterocolea* Grolle. Perhaps *Xenocephalozia* arose from an ancestor much like *C. trachyopa* through alteration of leaf insertion, loss of ornamentation, and reduction in plant size. I believe, however, that the narrow, transverse to weakly incubous leaf insertion of *Xenocephalozia* is a fundamental difference from *Clasmatocolea* and necessitates an independent generic status.

Variation.—Leaves of weak forms of this species tend to be entire margined and shallowly bilobed. The segments are short and rather wide-triangular, with the apex narrowly rounded or sometimes obtuse, and without development of a uniseriate row of cells. In fact, these phenotypes sometimes have leaves retuse or with a broadly lunate sinus. Well-developed axes, on the other hand, tend to have leaves with several spinose teeth on the dorsal margin and apices more deeply bilobed. In such plants the segments are ± acuminate, often apiculate, and have a uniseriate row of several cells. The former phase is illustrated in Schuster (1965b, f. II-8) and in the Stephani Icones (*Lophocolea* no. 92[a]), whereas the latter is also illustrated in the Stephani Icones (*Lophocolea* no. 92[b]) and in Massalongo (1906), who described the plant as a species of *Drepanolejeunea.*

Ecology.—A corticolous species mainly of Valdivian forests, occurring on tree or, less often, shrub trunks. It is comparable to *C. gayana* in usually occurring where there is a minimal amount of competition with other bryophytes and commonly does not occur on trunks or branches covered or festooned with large, thick masses of bryophytes. *Xenocepha-*

lozia navicularis is sometimes mixed with other hepatics, such as *C. ctenophylla*, *C. cucullistipula*, *C. humilis* var. *suspecta*, and *Lophocolea muricata*.

Phytogeography.—Nearly exclusively a Valdivian species (sea level-1,235 m.), occurring from R. Aisén (45° 25′ S.) N. to Prov. Arauco (37° 58′ S.); also Andean Patagonia at 800 m. in Parque Nac. Nahuel Huapí. Also known from one station in the Magellanian region—S. Skyring, Cabo Leon (Engel, 1973c).

Specimens seen.—**CHILE.** PROV. MAGALLANES: Cabo Leon, *Hatcher 44-3* (UW-M). PROV. AISÉN: R. Aisén, *Dusén s.n.* as syntype of *L. navicularis* — c. ♂ (NY); ibid., *Dusén 215* as *Cephalozia trisetosa* Steph., **nom. hb.** (UPS); ibid., *Dusén 225*, *237* — c. ♂ as syntype of *L. cucullistipula* (G); ibid., (*Dusén*) *237* as syntype of *L. navicularis* (G); ibid., *Dusén 288* as syntype of *L. navicularis* (FH, G — c. per.); ibid., *Dusén 301* as syntype of *L. navicularis* (BM); ibid., *Dusén 419* as syntype of *L. navicularis* (FH, JE — c. per., NY); Puerto Aisén, *Schuster s.n.* — c. per. + ♂ (hb. Grolle). PROV. CHILOÉ: I. Chiloé, Cord. San Pedro, Butalcura near R. Butalcura, 11 km. by road from Ruta 5, 100 m., *Engel 11830* (F). PROV. LLANQUIHUE: R. Puelo, S. Reloncavi, *Schwabe s.n.*, *5d*, *5i*, *11c* — c. per. (JE); Puerto Montt, *Dusén s.n.* — c. ♂ (hb. Grolle). PROV. LLANQUIHUE/PROV. OSORNO: L. Llanquihue, *Dusén s.n.* as *L. cucullistipula* (LD). PROV. OSORNO: 12.1 km. by road below Refugio Antillanca, 550 m., *Engel 11543B* — c. ♂, *11548* (F); around L. Toro on road to Refugio Antillanca, 855-885 m., *Engel 3992B*, *4009C*, *4025B*, *4052* (MSC); ibid., *Imshaug 42963* — c. sporo. (MSC); Termas de Puyehue, *Schwabe 64* (hb. Grolle, JE); ibid., *Schwabe 64 p.p.* (JE); ibid., 700 m., *Schwabe 68 p.p.* (JE). PROV. VALDIVIA: L. Ranco, 80 m., *Kubitzki 153* (hb. Grolle); W. slope of Cord. Pelada, W. of El Mirador, between La Union and Pta. Hueicolla, 580-680 m., *Engel 12259* — c. ♂, *12264*, *12317* (F); E. slope of Cord. Pelada, E. of El Mirador, between La Union and Pta. Hueicolla, 740-840 m., *Engel 12473* — c. per., *12477*, *12414* (F); near R. Futa in vicinity of Futa, 5.9 km. by road S. of junction of highway T-60 and T-65, near sea level, *Engel 10819* — c. per. (F); C. Lungoico, 500 m., *Schwabe 25 f*, *HCH110/c* (JE); Forestal Trafún, *Engel 11107*, *11108* (F); R. Llancahue, *Schwabe 10 p.p.* (JE); SW slope of V. Quetrupillán, 1,160-1,235 m., *Engel 11172* (F). PROV. CAUTÍN: Termas de Palguín, along R. Palguín, 730 m., *Engel 11344* (F). PROV. ARAUCO: Western foothills of Cord. Nahuelbuta, ridge S. of C. Lanalhue, SW of L. Lanalhue, 200 m., *Engel 12571* (F). **ARGENTINA.** PROV. RÍO NEGRO: Parque Nac. Nahuel Huapí, A. Frias, ca. 800 m., *Donat 31 p.p.* (JE).

Patagonia: *Sin. loc.*, *Dusén 215* — c. per., *288*, *301*, *419*, *440*, *441*, *463* as syntype of *L. navicularis* (G); ibid., *Dusén 288* — c. per. (FH).

11. **Clasmatocolea paucistipula** (Rodw.) Grolle.

Lophocolea paucistipula Rodw. Pap. & Proc. Roy. Soc. Tasmania 1916:46. 1917 (seors. 11 July 1916) (see also vol. 2 of *Tasmanian Bryophyta* p. 46. 1916). *Clasmatocolea paucistipula* (Rodw.) Grolle, Rev. Bryol. Lichénol. 29:72. 1960. *Hepatostolonophora paucistipula* (Rodw.) Engel, J. Hattori Bot. Lab. 46:103. 1979. Original material: Tasmania, near Cradle Mt., *Rodway* (hb. Grolle! — c. ♂, HO!). (Lophocoleaceae).

See Engel 1979b.

12. **Clasmatocolea planifolia** Steph., *nom. herb.*

Clasmatocolea planifolia Steph. *in herb. et icon. ined. Cephaloziella planifolia* Steph. *ex* Grolle, Rev. Bryol. Lichénol. 29:89. 1960 *non C. planifolia* Steph. Hedwigia 32:317. 1893. *Cephaloziella novae-caledoniae* Grolle, *nom. nov.*, Rev. Bryol. Lichénol. 29:208. 1960. *Cylindrocolea novae-caledoniae* (Grolle) Schust. Nova Hedwigia 22:161. 1972. Holotype: New Caledonia, Ile du Pin, 1909, *Le Rat* (M!). (Cephaloziellaceae).

See Grolle (1960) and Schuster (1972b) for taxonomic treatments; the former author includes illustrations (pl. II). See also the note in Fulford (1976, p. 401).

13. **Clasmatocolea rotata** (Hook. f. & Tayl.) Grolle.

Jungermannia rotata Hook. f. & Tayl. London J. Bot. 3:560. 1844. *Solenostoma rotatum* (Hook. f. & Tayl.) Mitt. *in* Hook. f. Handb. New Zealand Fl. p. 753. 1867, *nom. inval. Solenostoma rotatum* (Hook. f. & Tayl.) Mitt. *ex* Bastow, Pap. & Proc. Roy. Soc. Tasmania 1887:234. 1888. *Aplozia rotata* (Hook. f. & Tayl.) Rodw. Pap. & Proc. Roy. Soc. Tasmania 1916:81. 1917 (see also vol. 2 of *Tasmanian Bryophyta* p. 31. 1916). *Clasmatocolea rotata* (Hook. f. & Tayl.) Grolle, Oesterr. Bot. Z. 117:1. 1969. *Hepatostolonophora rotata* (Hook. f. & Tayl.) Engel, J. Hattori Bot. Lab. 46:98. 1979. Original material: New Zealand, *Hooker* (S!).

Aplozia alpina Rodw. Pap. & Proc. Roy. Soc. Tasmania 1915:106. 1916 (seors. 31 December 1915) (see also vol. 2 of *Tasmanian Bryophyta* p. 32. 1916), *syn. fide* Grolle (1969). *Clasmatocolea alpina* (Rodw.) Grolle, J. Jap. Bot. 41:226. 1966. Original material: Tasmania, Mt.

Wellington plateau, January 1915, *Rodway s.n.* (hb. Grolle!, HO!, MANCH! — c. per.).

Lophocolea zotovii Herz. Trans. & Proc. Roy. Soc. New Zealand 65:354. 1935, *syn. fide* Grolle (1969). *Clasmatocolea zotovii* (Herz.) Grolle, Rev. Bryol. Lichénol. 29:73. 1960. Holotype: New Zealand, North Island, Tararua Mts., Mt. Hector, ca. 1,310 m., 31 December 1933, *Zotov s.n.*, "Herb. P. R. S. H. 7499" (JE!; isotypes: CHR! — Hodgson hb. no. 478, hb. Grolle!). (Lophocoleaceae).

See Engel (1979b).

14. **Clasmatocolea truncata** Steph.

Clasmatocolea truncata Steph. Bull. Herb. Boissier 5:87. 1897 ≡ *Pedinophyllum interruptum* subsp. *truncatum* (Steph.) H. Inoue, J. Hattori Bot. Lab. 19:33. 1958. Original material: Japan, Hokkaido, 1894, *Faurie 12606* (*non vidi*). (Plagiochilaceae).

See Hattori (1950), who removed the species from *Clasmatocolea*, Inoue (1958) for illustrations, and Grolle (1956, p. 294).

Specimen seen.—Japan, *Faurie 12602* (FH—hb. Steph.).

15. **Clasmatocolea typhacella** Steph., *nom. nud.*

Clasmatocolea typhacella Steph. *in* Grolle, Rev. Bryol. Lichénol. 25:301. 1956, *nom. nud. pro syn.* = *Myriocoleopsis puiggari* Schiffn. Hedwigia 81:235. *pl. 1.* 1944. (Lejeuneaceae).

See Grolle (1956, p. 301) and Gradstein & Vital (1975).

Specimen seen.—**BRAZIL.** ESTADO DE SÃO PAULO: Iporanga, *Puiggari* (FH—hb. Steph.!, M!).

REFERENCES

American Geographical Society of New York

1945. American Geographical Society map of Hispanic America, publication no. 5. Index to map of Hispanic America; 1: 1,000,000. Washington, D.C., pp. 1-923.

Arnell, S.

1955a. Hepaticae of Chile and Argentina collected by R. Santesson. Svensk Bot. Tidskr., **49,** pp. 229-239, figs. 1-2.

1955b. Notes on South African hepatics II. Bot. Not., **108,** pp. 309-313.

1958. Genus *Jungermannia* in South Africa. Bot. Not., **111,** pp. 619-622, figs. 1-2.

1963. Hepaticae of South Africa. Stockholm, pp. 1-411, figs. 1-290.

Berggren, S.

1898. On New Zealand Hepaticae. E. Malström, Lund, pp. 1-48, figs. 1-32.

Bescherelle, E. and C. Massalongo

1889. Muscinées. I.—Hépatiques. Mission Sci. Cap Horn, 1882-1883, **5,** pp. 201-252, pl. 1-5.

Dietz, R. S. and J. C. Holden

1970a. The breakup of Pangaea. Sci. Amer., **223**(4), pp. 30-41.

1970b. Reconstruction of Pangaea: Breakup and dispersion of continents, Permian to Present. J. Geophys. Res., **75,** pp. 4939-4956.

Engel, J. J.

1973a. *Chiloscyphus hookeri* n. sp. and nomenclatural changes in the genus *Clasmatocolea.* J. Hattori Bot. Lab., **36,** pp. 150-156, figs. 1-2 (1972).

1973b. On the typification of *Austrolophozia fuegiensis* (Steph.) Schust. J. Hattori Bot. Lab., **37,** pp. 181-183.

1973c. The Raymond E. Hatcher collection of Hepaticae and Anthocerotae from southern South America, with new taxa and notes on range extensions. Bryologist, **76,** pp. 528-535, figs. 1-18.

1976. On the typification of *Clasmatocolea obvoluta* (Hook. f. & Tayl.) Grolle (Hepaticae). Misc. Bryol. Lichenol., **7,** p. 75.

1978. A taxonomic and phytogeographic study of Brunswick Peninsula (Strait of Magellan) Hepaticae and Anthocerotae. Fieldiana, Bot., **41,** pp. 1-319.

1979a. Austral Hepaticae XI. Lophocoleaceae: New taxa, new combinations and realignments. Phytologia, **41,** pp. 309-312.

1979b. Austral Hepaticae X. A revision of *Hepatostolonophora* Engel & Schust., nom. nov. (Hepaticae). J. Hattori Bot. Lab., **46,** pp. 91-108, figs. 1-8.

1980. Austral Hepaticae XII. A new species of *Clasmatocolea* (Hepaticae) from Tasmania. Bryologist, **83,** pp. 220-223, figs. 1-19.

Engel, J. J. and R. M. Schuster

1975. Austral Hepaticae III. *Stolonophora,* a new genus of Geocalycaceae. Fieldiana, Bot., **36,** pp. 111-124, figs. 1-6.

Evans, A. W.
1939. The classification of the Hepaticae. Bot. Rev. (Lancaster), **5,** pp. 49-96.
Frye, T. C. and L. Clark
1943. Hepaticae of North America. Part II. Univ. Wash. Publ. Biol., **6**(2), pp. 163-334.
Fulford, M.
1965. Evolutionary trends and convergence in the Hepaticae. Bryologist, **68,** pp. 1-31, figs. 1-65.
1976. Manual of the leafy Hepaticae of Latin America. Part IV. Mem. New York Bot. Gard., **11,** pp. 393-535, pl. 108-159.
Gola, G.
1923. Le epatiche raccolte dal Dott. G. B. de Gasperi nella Terra del Fuoco sud-occidentale. Nuovo Giorn. Bot. Ital., II., **29,** pp. 162-173.
Gottsche, C. M., J. B. G. Lindenberg and C. G. Nees ab Esenbeck
1844-47. Synopsis Hepaticarum. Hamburg, pp. i-xxvi, 1-834.
Gradstein, S. R., A. M. Cleef and M. H. Fulford
1977. Studies on Colombian cryptogams IIA. Hepaticae—Oil body structure and ecological distribution of selected species of tropical Andean Jungermanniales. Proc. Koninklijke Ned. Akad. Wetensch., Amsterdam, ser. C., **80,** pp. 377-420, pl. 1-5, map 1.
Gradstein, S. R. and D. M. Vital
1975. On *Myriocoleopsis* Schiffn. (Lejeuneaceae). Lindbergia, **3,** pp. 39-45, figs. 1-16, photo 1.
Greene, S. W.
1964. Plants of the land, pp. 240-253, figs. 1-9. *In* Priestley, R., R. Adie, and G. de Q. Robin, eds., Antarctic research. A review of British scientific achievement in Antarctica. Butterworths, London.
Grolle, R.
1956. Revision der *Clasmatocolea*-Arten. Rev. Bryol. Lichénol., **25,** pp. 288-303, pl. 1-3.
1959. Beitrag zur Kenntnis der afrikanischen Lophocoleen. Trans. Brit. Bryol. Soc., **3,** pp. 582-598, pl. 1-3.
1960. Nachtrag zur "Revision der *Clasmatocolea*-Arten." Rev. Bryol. Lichénol., **29,** pp. 68-91, pl. 1-3, map 1.
1962. Monographie der Lebermoosgattung *Leptoscyphus* Mitt. Nova Acta Leop., **25**(161), pp. 1-143, pl. 1-25, maps 1-6.
1964. *Neesioscyphus*—eine neue Lebermoosgattung mit gedrehten Sporogonklappen. Oesterr. Bot. Z., **111,** pp. 19-36, figs. 1-5.
1965. *Wettsteinia* Schiffn. J. Hattori Bot. Lab., **28,** pp. 94-100, pl. 1-3.
1966. Miscellanea hepaticologica (61-70). J. Jap. Bot., **41,** pp. 225-232, figs. 1-2.
1969. Miscellanea hepaticologica 101-110. Oesterr. Bot. Z., **117,** pp. 1-6, fig. 1.
1971. *Jamesoniella* und verwandte. Feddes Repert., **82,** pp. 1-100, pl. 1-23.
1972a. Zur Kenntnis von *Adelanthus* Mitt. J. Hattori Bot. Lab., **35,** pp. 325-370, pl. 1-11.
1972b. The hepatics of the South Sandwich Islands and South Georgia. Brit. Antarc. Surv. Bull., **28,** pp. 83-95, fig. 1, tab. 1.
Hamlin, B. G.
1972. Hepaticae of New Zealand, Parts I and II. Index of binomials and preliminary checklist. Rec. Domin. Mus., **7,** pp. 243-366.
1973. Hepaticae of New Zealand, Part III. Additions and corrections to the index of binomials. Rec. Domin. Mus., **8,** pp. 139-152.

Hässel de Menéndez, G. G.
1977. Liverworts new to South Georgia. Brit. Antarc. Surv. Bull., **46,** pp. 99-108.
Hattori, S.
1950. Notulae de Hepaticis Japonicis (11). J. Jap. Bot., **25,** pp. 46-51, fig. 55.
Herzog, T.
1921. Die Bryophyten meiner zweiten Reise durch Bolivia. Biblioth. Bot., **21**(88), pp. 1-31, figs. 1-19 (Hepaticae, pp. 26-31; 1920).
1939. I. Verzeichnis der gesammelten Bryophyten, pp. 1-35, figs. 1-10. *In* Herzog, T., G. H. Schwabe, and E. Schwabe, Zur Bryophytenflora Südchiles, Beih. Bot. Centralbl., **60B**(1-2).
1943. Eine kleine Lebermoos-Sammlung aus Chile. Acta Horti Gothob., **15,** pp. 157-162, fig. 1.
1952. Miscellanea bryologica. III. Memoranda Soc. Fauna Fl. Fenn, **27,** pp. 92-110, figs. 39-50 (1951).
1954. Zur Bryophytenflora Chiles. Rev. Bryol. Lichénol., **23,** pp. 27-99, figs. 1-24 (Hepaticae, pp. 28-66).
Herzog, T. and A. Noguchi
1955. Bietrag zur Kenntnis der Bryophytenflora von Formosa und den benachbarten Inseln Botel Tobago und Kwashyota. J. Hattori Bot. Lab., **14,** pp. 29-70, figs. 1-23 (Hepaticae, pp. 29-55).
Hodgson, E. A.
1946. New Zealand Hepaticae (Liverworts). V. The family Jungermanniaceae. Trans. & Proc. Roy. Soc. New Zealand, **76,** pp. 68-86.
1953. New Zealand Hepaticae (Liverworts)—VII. A review of the New Zealand species of the genus *Lophocolea* with notes on *Chiloscyphus*. Trans. Roy. Soc. New Zealand, **80,** pp. 329-358, pl. 75-77.
1962. Hepatics from the subantarctic islands of New Zealand including "Cape Expedition" collections from the Auckland and Campbell Islands. Rec. Domin. Mus., **4,** pp. 101-132.
Holmgren, P. K. and W. Keuken
1974. Index Herbariorum. Part I. The herbaria of the world. 6th ed. Utrecht, pp. i-vii, 1-397.
Hooker, J. D. and T. Taylor
1844. Hepaticae antarcticae; being characters and brief descriptions of the Hepaticae discovered in the southern circumpolar regions during the voyage of H. M. Discovery Ships *Erebus* and *Terror*. London J. Bot., **3,** pp. 366-400; 454-481; 556-582.
Hueck, K.
1966. Die Wälder Südamerikas. Ökologie, Zusammensetzung und wirtschaftliche Bedeutung. Gustav Fisher, Stuttgart, pp. i-xviii, 1-422, figs. 1-253.
Inoue, H.
1958. The family Plagiochilaceae of Japan and Formosa. I. J. Hattori Bot. Lab., **19,** pp. 25-59, figs. I-XI.
Kuschel, G.
1960. Terrestrial zoology in southern Chile. Proc. Roy. Soc. London, Ser. B, Biol. Sci., **152,** pp. 540-550, fig. 1.
Leistner, O. A. and J. W. Morris
1976. Southern African place names. Ann. Cape Prov. Mus., **12,** pp. 1-565.
Massalongo, C.
1906. Epatiche della Repubblica Argentina raccolte dal Prof. C. Spegazzini. Atti Accad. Sci. Med. Nat. Ferrara, **80,** pp. 7-18, figs. 1-15.

MITTEN, W.
1877. List of Hepaticae collected by the Rev. A. E. Eaton at the Cape of Good Hope (August and September 1874). J. Linn. Soc., Bot., **16,** pp. 187-196, pl. 4-5.
1879. III. Hepaticae. Philos. Trans., **168** (extra vol.), pp. 40-45.
MIZUTANI, M. AND S. HATTORI
1959. On some little known species of *Lophocolea* (Hepaticae) from the Southern Hemisphere. J. Jap. Bot., **34,** pp. 167-173, figs. I-II.
MOORE, D. M.
1968. The vascular flora of the Falkland Islands. Brit. Antarc. Surv. Sci. Rep., **60,** pp. 1-202, pl. 1-6, maps 1-2.
MÜLLER, K.
1939-1940. Die Lebermoose (Musci hepatici). *In* Rabenhorst's Kryptogamen-Flora. VI. Ergänzungsband. Fasc. **1,** pp. 1-160 (1939); Fasc. **2,** pp. 161-320 (1940).
1951-1958. Die Lebermoose Europas. *In* Rabenhorst's Kryptogamen-Flora, ed. 3, 6, pp. 1-1,365, figs. 1-514. Leipzig.
NEW ZEALAND. DEPARTMENT OF LANDS AND SURVEY
1968. Gazetteer of New Zealand place names. Wellington, pp. i-xii, 1-576.
ODU, E. AND P. W. RICHARDS
1976. The stimulus to branching of the rhizoid tip in *Lophocolea cuspidata* (Nees) Limpr. J. Bryol., **9,** pp. 93-95, fig. 1.
PEARSON, W. H.
1922. Note on *Jungermannia humilis*. Bull. Misc. Inform., **1922,** pp. 248-253, pl. 1-4.
RAVEN, P. H. AND D. I. AXELROD
1972. Plate tectonics and Australasian paleobiogeography. Science, **176,** pp. 1379-1386.
1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard., **61,** pp. 539-673.
RODWAY, L.
1916. Tasmanian Bryophyta. Vol. II. Hepatics, pp. i-vii, 1-95 (issued separately on 30 August 1916); appeared as *Tasmanian Bryophyta* in Pap. & Proc. Roy. Soc. Tasmania, **1916,** pp. 51-143 (19 February 1917) but without preface, glossary, and appendix of separate.
SAYRE, G., C. E. B. BONNER AND W. L. CULBERSON
1964. The authorities for the epithets of mosses, hepatics, and lichens. Bryologist, **67,** pp. 113-135.
SCHIFFNER, V.
1893. Hepaticae (Lebermoose), pp. 3-141, figs. 1-73. *In* Engler, A., and K. Prantl, eds., Die Natürlichen Pflanzenfamilien, Teil I, Abt. 3. Leipzig.
1912. Über *Nardia Lindmanii* Steph. Hedwigia, **51,** pp. 273-277.
SCHOPF, J. M.
1970. Relation of floras of the Southern Hemisphere to continental drift. Taxon, **19,** pp. 657-674.
SCHUSTER, R. M.
1958. Notes on nearctic Hepaticae, XIV. The Chonecoleaceae. J. Hattori Bot. Lab., **20,** pp. 1-16, figs. 1-2.
1963. Studies on antipodal Hepaticae. I. Annotated keys to the genera of antipodal Hepaticae with special references to New Zealand and Tasmania. J. Hattori Bot. Lab., **26,** pp. 185-309.
1965a. Studies on Hepaticae XXVI. The *Bonneria-Paracromastigum-Pseudocephalozia-*

Hyalolepidozia-Zoopsis-Pteropsiella complex and its allies: a phylogenetic study (part 1). Nova Hedwigia, **10,** pp. 19-61.

1965b. Studies on Hepaticae, XXVII. *Xenocephalozia* Schust. J. Hattori Bot. Lab., **28,** pp. 139-145, figs. 1-2.

1966. The Hepaticae and Anthocerotae of North America east of the hundredth meridian. Vol. 1. Columbia University Press, N.Y., pp. i-xvii, 1-802, figs. 1-48.

1967. A memoir of the family Blepharostomataceae, II. Candollea, **21,** pp. 241-355, figs. 22-50 (1966).

1969. Problems of antipodal distribution in lower land plants. Taxon, **18,** pp. 46-91, maps 1-24.

1972a. Continental movements, "Wallace's Line" and Indomalayan-Australasian dispersal of land plants: some eclectic concepts. Bot. Rev. (Lancaster), **38,** pp. 3-86.

1972b. Studies on Cephaloziellaceae. Nova Hedwigia, **22,** pp. 121-265, pl. 1-25 (1971).

SCHUSTER, R. M. AND J. J. ENGEL

1973. Austral Hepaticae II. *Evansianthus*, a new genus of Geocalycaceae. Bryologist, **76,** pp. 516-520, figs. 1-9.

1977. Austral Hepaticae, V. The Schistochilaceae of South America. J. Hattori Bot. Lab., **42,** pp. 273-423, figs. 1-45.

SIM, T. R.

1926. The Bryophyta of South Africa comprising Sphaerocarpales, Marchantiales, Jungermanniales, Anthocerotales, Sphagnales, Andreaeales, Polyrichales, Bryales. Trans. Roy. Soc. South Africa, **15,** pp. 1-475.

SKOTTSBERG, C.

1910. Botanische Ergebnisse der schwedischen Expedition nach Patagonien und dem Feuerlande 1907-1909. I. Übersicht über die wichtigsten Pflanzenformationen Südamerikas S. von 41°, ihre geographische Verbreitung und Beziehungen zum Klima. Kongl. Svenska Vetenskapsakad. Handl., **46**(3), pp. 1-28, 1 map.

1916. Botanische Ergebnisse der schwedischen Expedition nach Patagonien und dem Feuerlande 1907-1909. V. Die Vegetationsverhältnisse längs der Cordillera de los Andes S. von 41° S. br. Ein Beitrag zur Kenntnis der Vegetation in Chiloé, Westpatagonien, dem Andinen Patagonien und Feuerland. Kongl. Svenska Vetenskapsakad Handl., **56**(5), pp. 1-366, figs. 1-24, pl. 1-23.

SMITH, A. G. AND A. HALLAM

1970. The fit of the southern continents. Nature, **225,** pp. 139-144.

SORSA, P. AND T. KOPONEN

1973. Spore morphology of Mniaceae Mitt. (Bryophyta) and its taxonomic significance. Ann. Bot. Fenn., **10,** pp. 187-200, figs. 1-6.

SPRUCE, R.

1884-1885. Hepaticae Amazonicae et Andinae. Trans. & Proc. Bot. Soc. Edinburgh, **15,** pp. 1-308, pl. 1-4, 1884 (part I); pp. i-xi, 309-589, pl. 5-22, 1885 (part II).

STEPHANI, F.

1897. Die Lebermoose der ersten Regnell'schen Expedition nach Südamerika. Bih. Kongl. Svenska Vetensk.-Akad. Handl., **23**(III,2), pp. 3-36.

1898-1924. Species Hepaticarum. Genève & Bale, 6 vols.

1900. Beiträge zur Lebermoos-Flora Westpatagoniens und des südlichen Chile. Bih. Kongl. Svenska Vetensk.-Akad. Handl., **26**(III, 6), pp. 1-69.

1901. Lebermoose der Magellansländer. Bih. Kongl. Svenska Vetensk.-Akad. Handl., **26**(III, 17), pp. 1-36.

1911. II. Die Lebermoose. *In* Skottsberg, C., Botanische Ergebnisse der schwedischen

Expedition nach Patagonien und dem Feuerlande 1907-1909. Kongl. Svenska Vetenskapsakad. Handl., **46**(9), pp. 1-92, figs. 1-35.

1916. Hepaticae, pp. 173-268. *In* Herzog, T., Die Bryophyten meiner zweiten Reise durch Bolivia. Biblioth. Bot., **21**(87), pp. 1-347, figs. 1-234, pl. I-VIII, 1 map.

TAYLOR, T. AND J. D. HOOKER

1847. Ord. LIII. Hepaticae, Juss., pp. 423-446. *In* Hooker, J. D., The botany of the Antarctic voyage. Vol. I. Flora Antarctica. Part II. Botany of Fuegia, the Falkland's, Kerguelen's Land, etc.

TREVISAN DE SAINT-LÉON, V.

1877. Schema di una nuova classificazione delle epatiche. Mem. Ist. Lomb. Sci. Lett. III., **4**, pp. 383-451.

U.S. BOARD ON GEOGRAPHIC NAMES

1954. New Zealand. Washington, D.C., pp. i-ii, 1-454.

U.S. OFFICE OF GEOGRAPHY

1955. Peru: official standard names approved by the United States Board on Geographic Names. Washington, D.C., Central Intelligence Agency, pp. i-iii, 1-609.

1957. Australia . . . U.S. Board on Geographic Names, gazetteer No. 40. Washington, D.C., pp. i-iii, 1-750.

1963. Brazil . . . Washington, D.C., pp. i-v, 1-915.

1964. Colombia . . . U.S. Board on Geographic Names, gazetteer No. 86. Washington, D.C., pp. i-vi, 1-396.

1967. Chile . . . U.S. Board on Geographic Names, gazetteer No. 6. 2nd ed. Washington, D.C., pp. i-vii, 1-591.

1968. Argentina . . . U.S. Board on Geographic Names, gazetteer No. 103. Washington, D.C., pp. i-viii, 1-699.

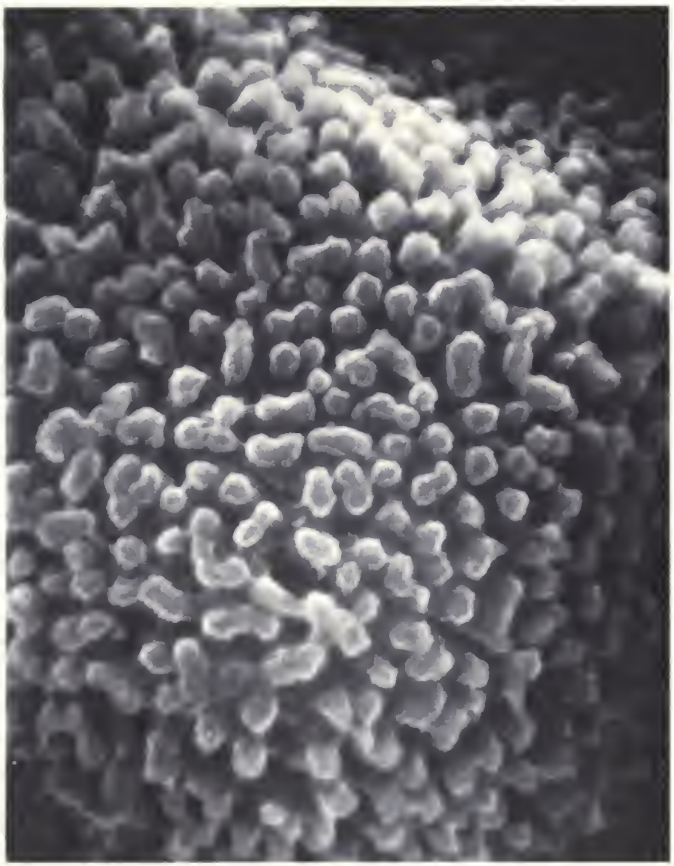
VÁŇA, J.

1975. Studien über die *Jungermannioideae* (Hepaticae) 9. *Jungermannia* Subg. *Plectocolea* und Subg. *Solenostoma* in Hawaii; Ergänzungen und Synopsis der Gattung *Jungermannia*. Folia Geobot. Phytotax., Praha, **10**, pp. 357-382, figs. 1-7.

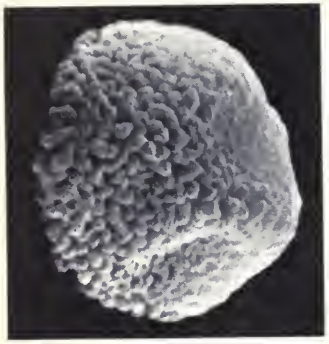
VERDOORN, F.

1932. Classification of hepatics, chap. XV, pp. 413-432. *In* Verdoorn, F., ed., Manual of Bryology. The Hague.

1. *Clasmatocolea rigens* (Hook. f. Tayl.) Engel. × 5,000; from *Engel 1359A*.



2. *Clasmatocolea rigens* (Hook. f. & Tayl.) Engel. × 10,000; from *Engel 1359A*.

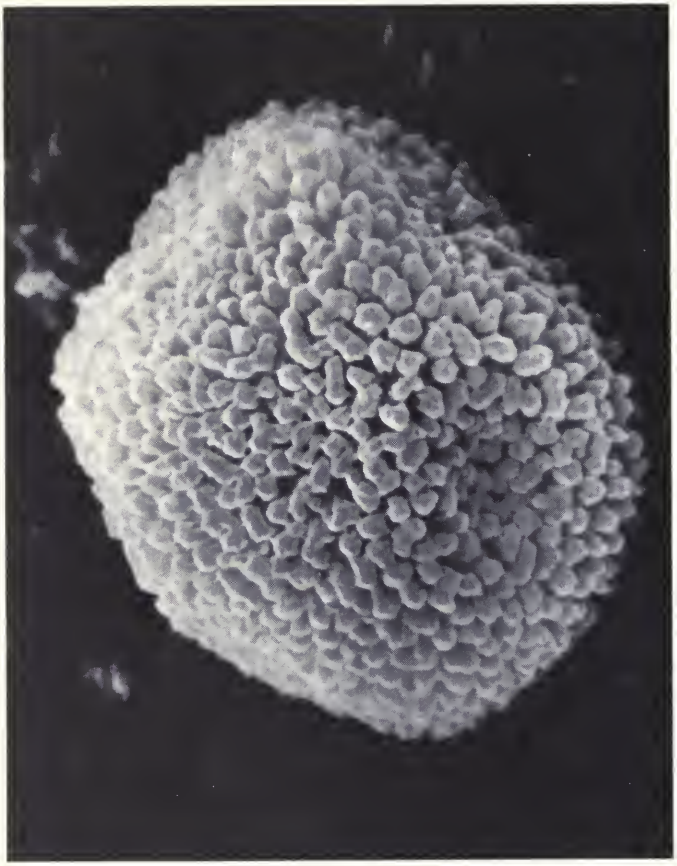


3. *Clasmatocolea obvoluta* (Hook. f. & Tayl.) Grolle. × 4,700; from *Engel 4574A*.

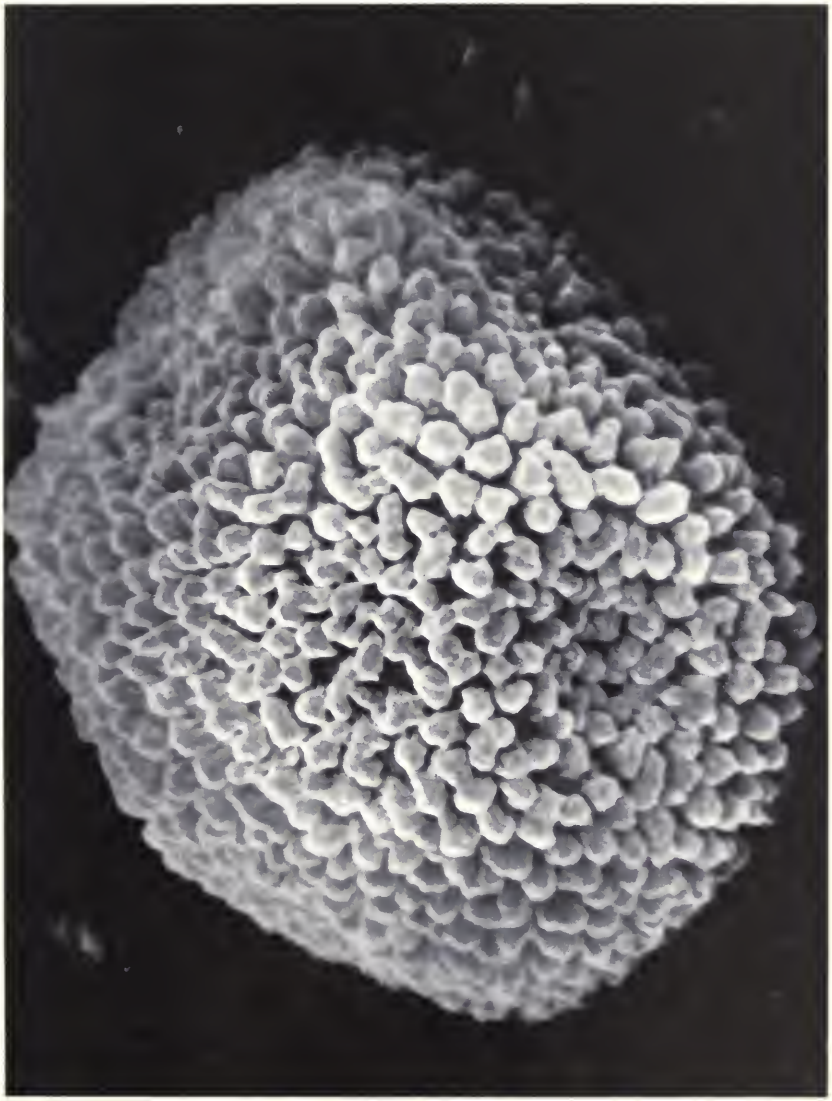
4. *Clasmatocolea obvoluta* (Hook. f. & Tayl.) Grolle. × 9,500; from *Engel 4574A*.

5. *Clasmatocolea trachyopa* (Hook. f. & Tayl.) Grolle. × 5,000; from *Engel 5151A*.

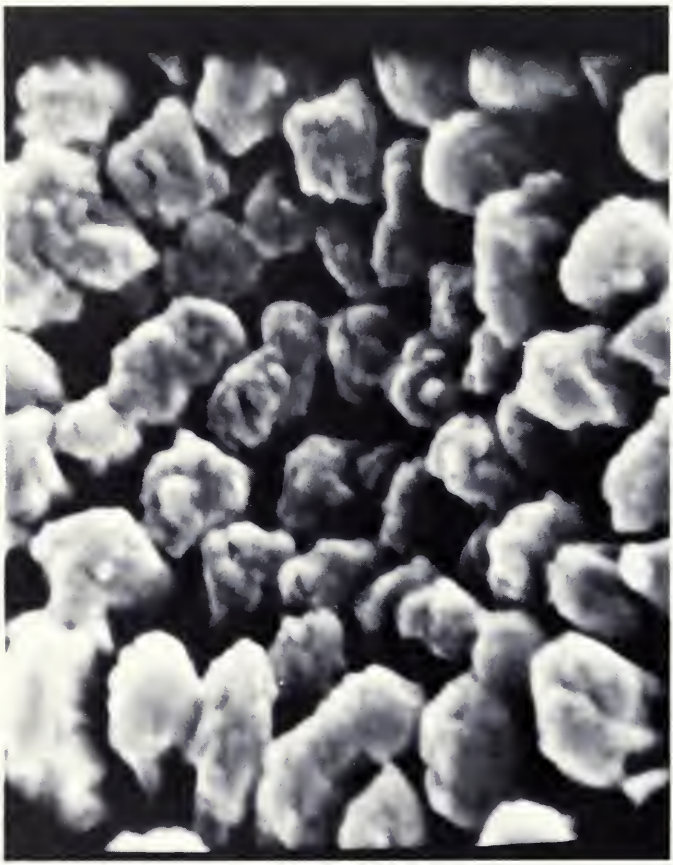
6. *Clasmatocolea trachyopa* (Hook. f. & Tayl.) Grolle. × 10,000; from *Engel 5151A*.



7. *Clasmatocolea humilis* (Hook. f. & Tayl.) Grolle. × 6,600; from *Engel 5472.*



8. *Clasmatocolea humilis* (Hook. f. & Tayl.) Grolle. × 9,700; from *Engel 5472*.



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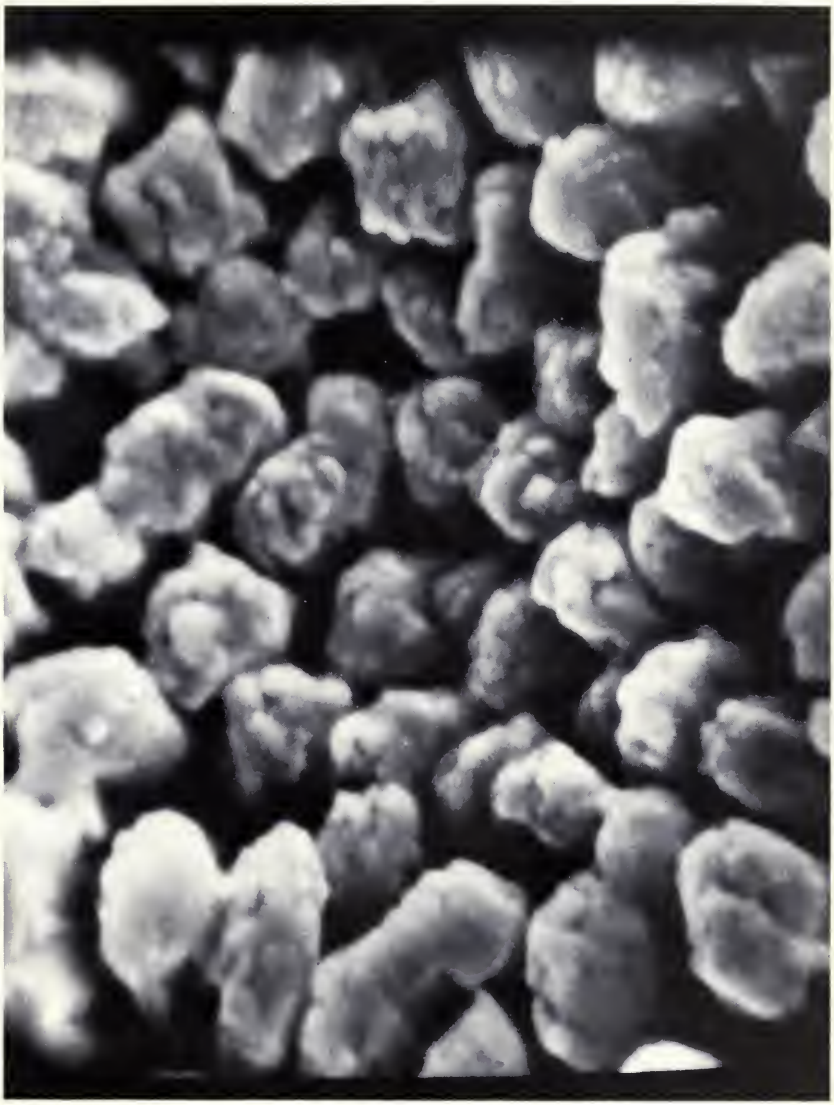

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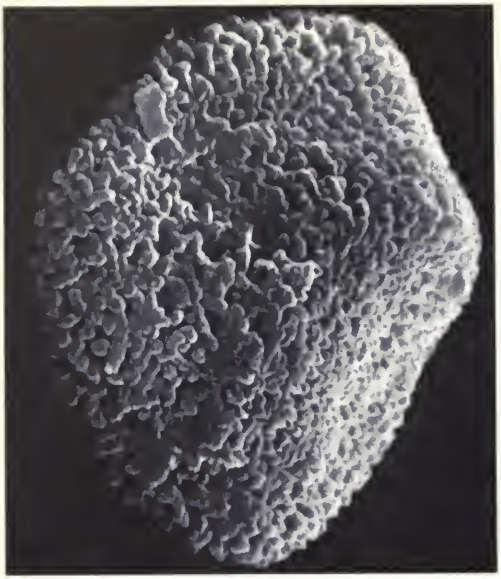
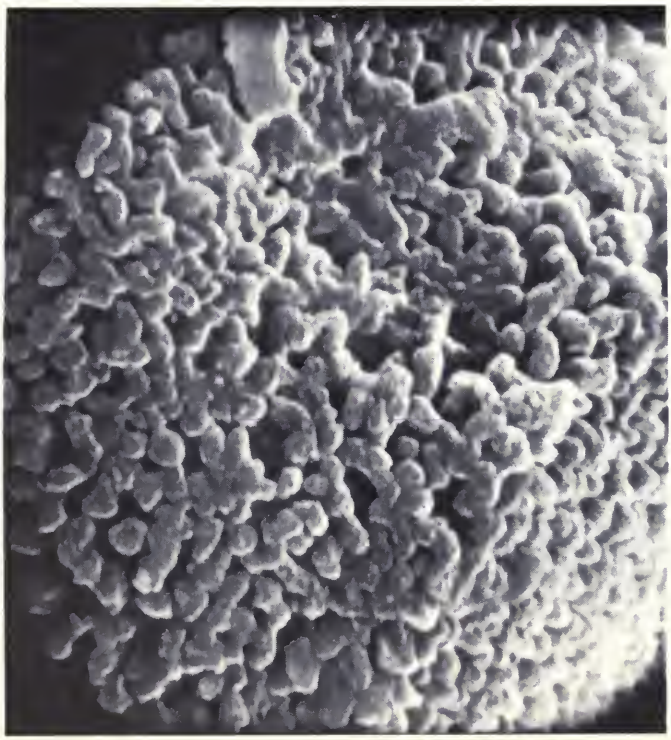


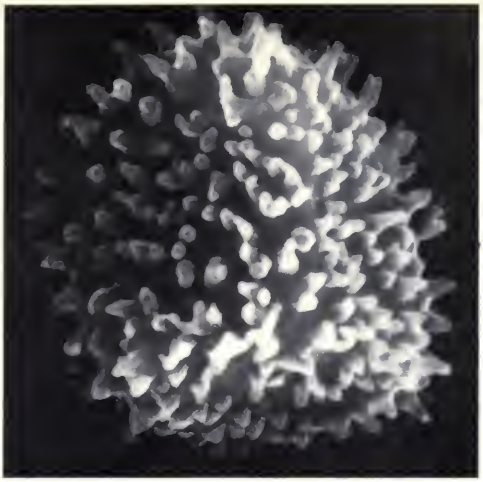
11. *Clasmatocolea vermicularis* (Lehm.) Grolle. × 5,000; from *Dusén 166*.



12. *Clasmatocolea vermicularis* (Lehm.) Grolle. × 10,000; from *Dusén 166*.

13. *Clasmatocolea gayana* (Mont.) Grolle. × 3,655; from *Engel 4554*.

14. *Clasmatocolea gayana* (Mont.) Grolle. × 10,260; from *Engel 4554*.



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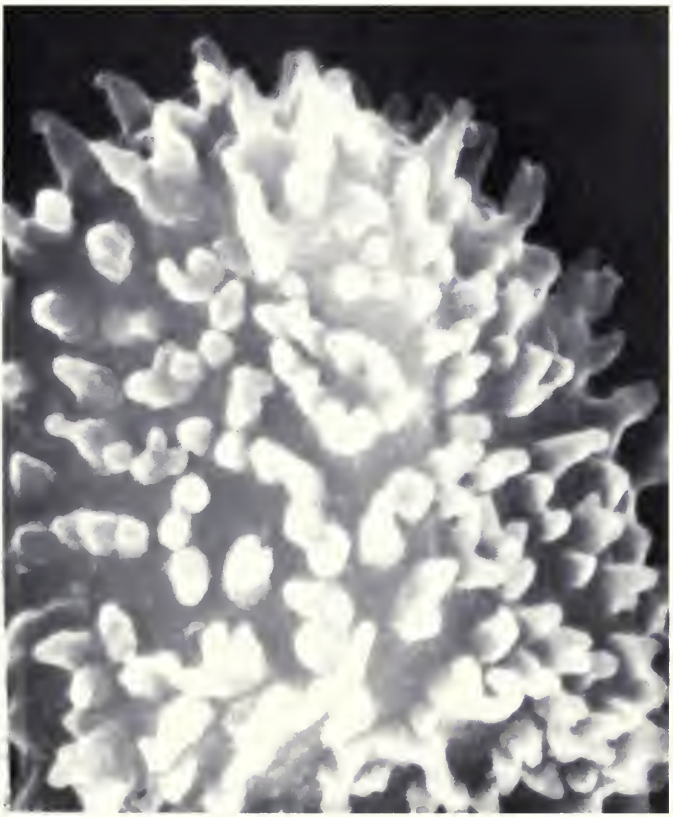
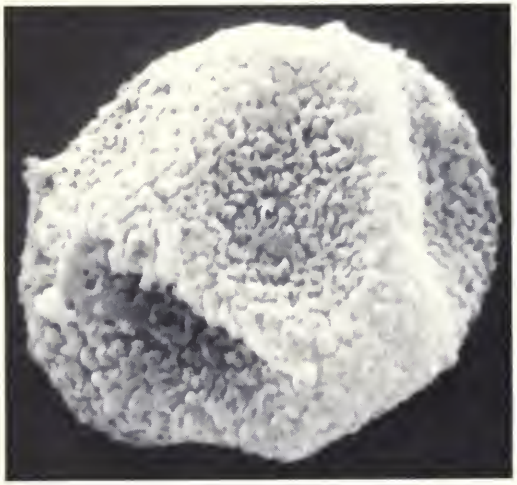
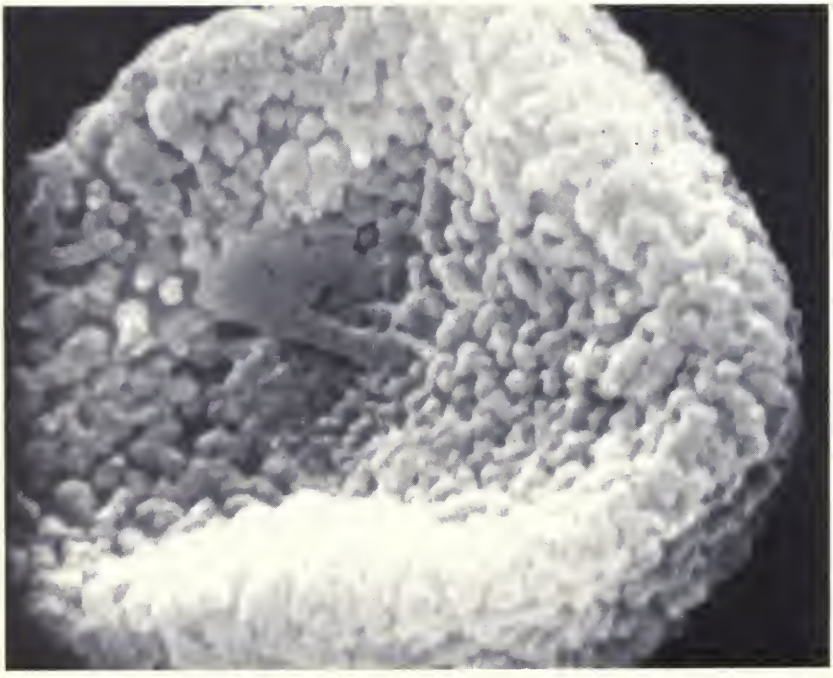


16. *Clasmatocolea ctenophylla* (Schiffn.) Grolle. × 10,000; from *Engel 5214.*

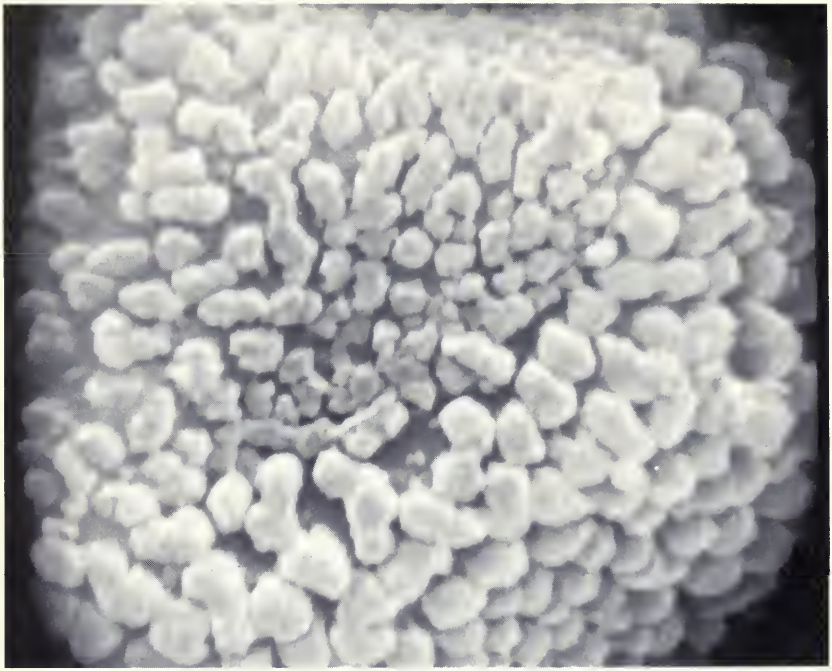


17. *Clasmatocolea minutiretis* Engel & Grolle. × 5,400; from *Engel 4785*.

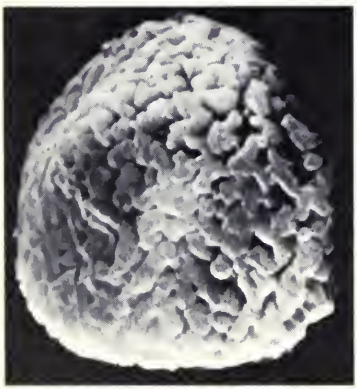


18. *Clasmatocolea minutiretis* Engel & Grolle. × 10,750; from *Engel 4785*.

19. *Clasmatocolea fulvella* (Hook. f. & Tayl.) Grolle. × 5,400; from *Engel 6125*.

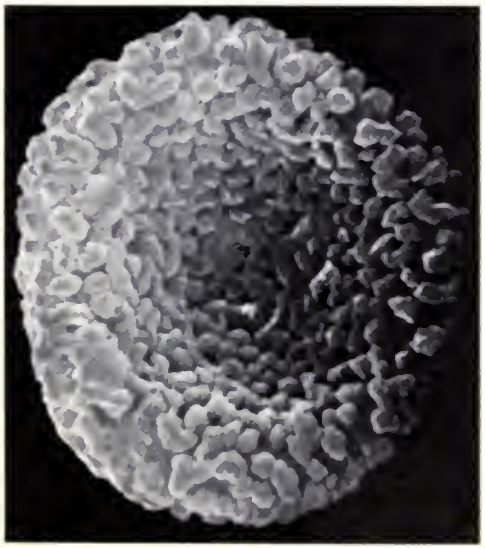


20. *Clasmatocolea fulvella* (Hook. f. & Tayl.) Grolle. × 10,750; from *Engel 6125*.

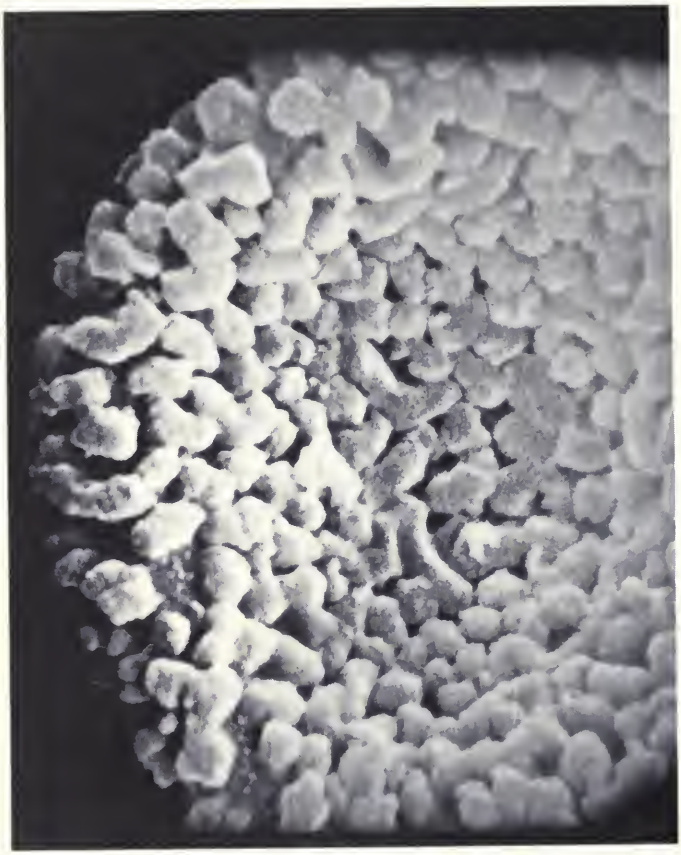


21. *Clasmatocolea strongylophylla* (Hook. f. & Tayl.) Grolle. × 5,240; from *Schuster 48481*.

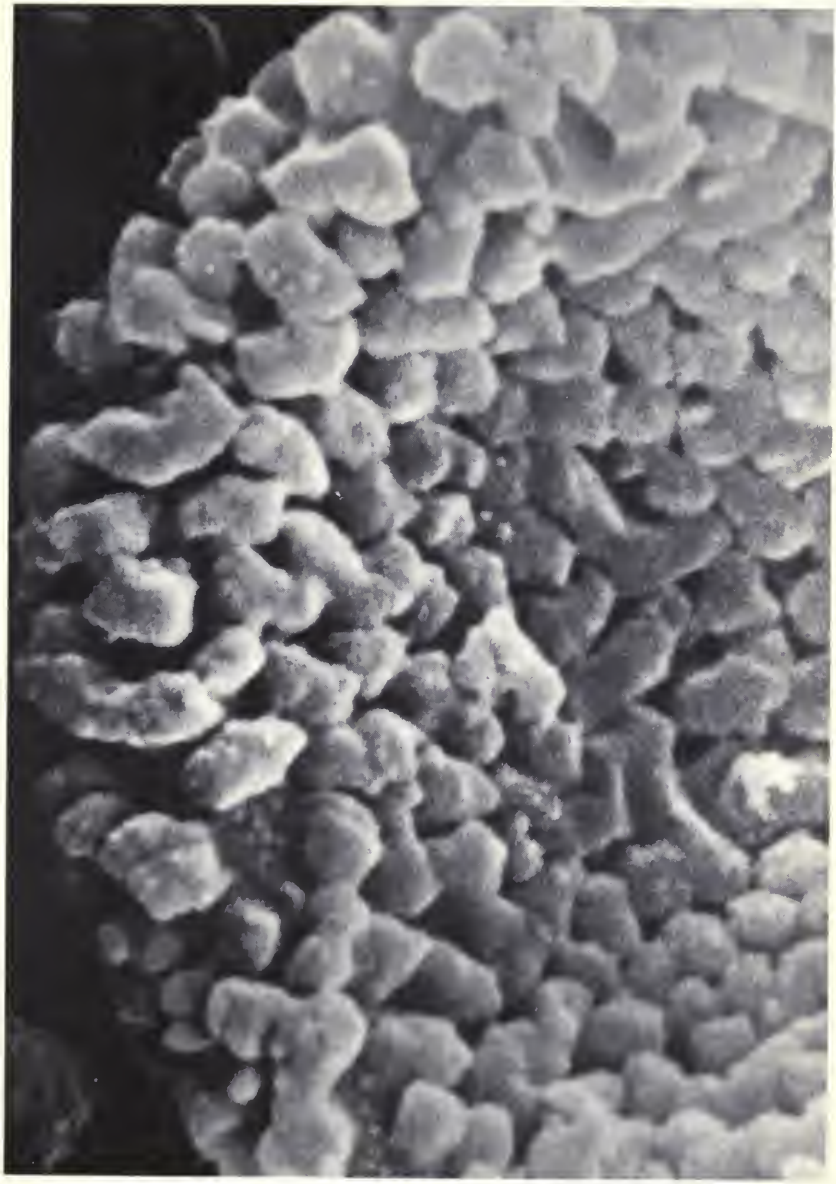
22. *Clasmatocolea strongylophylla* (Hook. f. & Tayl.) Grolle. × 10,000; from *Schuster 48481.*



23. *Clasmatocolea puccioana* (De Not.) Grolle. × 6,075; from *Engel 4520.*



24. *Clasmatocolea puccioana* (De Not.) Grolle. × 12,100; from *Engel 4520*.



25. *Clasmatocolea puccioana* (De Not.) Grolle. × 25,300; from *Engel 4520*.

26. *Clasmatocolea navistipula* (Steph.) Grolle. × 5,000; from *Engel 4251.*

27. *Clasmatocolea navistipula* (Steph.) Grolle. × 10,000; from *Engel 4251.*

28. *Clasmatocolea cucullistipula* (Steph.) Grolle. × 3,100; from *Dusén s.n.*, syntype of *L. cucullistipula*.

29. *Clasmatocolea cucullistipula* (Steph.) Grolle. × 10,200; from *Dusén s.n.*, syntype of *L. cucullistipula*.

INDEX OF TAXA

Recognized taxa are in roman type, illegitimate or synonymous taxa are italicized, and new taxa and new combinations are in boldface.

Alicularia flexuosa (Lehm.) Nees 97
Alicularia grandistipula Herz. 99
Alicularia grandistipula (Steph.) Horik. 99
Alicularia lindmanii (Steph.) Steph. 97
Alicularia strongylophylla (Hook. f. & Tayl.) G.L. & N. 147
Alicularia strongylophylla var. *minor* (Hook. f. & Tayl.) G. L. & N. 149
Alicularia vermicularis (Lehm.) G. L. & N. 96
Anomylia cuneifolia (Hook.) Schust. 191
Anthoscyphus tjiwideiensis (Sande-Lac.) Trev. 154
Aplozia alpina Rodw. 196
Aplozia cuneifolia (Hook.) Dum. 191
Aplozia rotata (Hook. f. & Tayl.) Rodw. 196

Blepharostoma acanthifolium Gola 60

Calyptrocolea perssonii Schust. 192
Cephalozia rigens (Hook. f. & Tayl.) Trev. 44
Cephalozia trisetosa Steph. 193
Cephaloziella novae-caledoniae Grolle 196
Cephaloziella planifolia Steph. (1893) 196
Cephaloziella planifolia Steph. *ex* Grolle 196
Chiloscyphus cordifolius Rodw. 173
Chiloscyphus fasciculatus (Nees) G. L. & N. 91
Chiloscyphus fasciculatus var. β *dregeana* Nees 91
Chiloscyphus fasciculatus var. γ *exarida* Nees 91
Chiloscyphus fulvellus (Hook. f. & Tayl.) Nees 139
Chiloscyphus gayanus (Mont.) G. L. & N. 112
Chiloscyphus nigrescens Lindenb. & Hampe 97
Chiloscyphus notophyllus (Hook. f. & Tayl.) G. L. & N. 173
Chiloscyphus rabenhorstii Steph. 91
Chiloscyphus tjiwideiensis Sande-Lac. 154
Chonecolea doellingeri (Nees) Grolle 191
Clasmatocolea Spruce 39
  Subg. Clasmatocolea 69
  Subg. Lacerfolia Steph. *ex* **Engel** 50
  Subg. Metaclasmatocolea Engel 157
  Subg. Plicaticalyx Engel 183
  Subg. Protoclasmatocolea Engel 44
  Subg. Squamicalyx Engel 173
  Sect. Clasmatocolea 74
  Sect. Fulvellae Engel 138
  Sect. Metaclasmatocolea 165
  Sect. Pachyclasmatocolea Engel 69
  Sect. Puccioanae Engel 157
  Sect. Strongylophyllae Engel 147

Clasmatocolea abnormis (Besch. & Mass.) Grolle 190
Clasmatocolea acutiloba Schiffn. 191
Clasmatocolea alpina (Rodw.) Grolle 196
Clasmatocolea angulistipula (Steph.) Grolle 149
Clasmatocolea chilensis Steph. 97
Clasmatocolea cookiana (Mass.) Engel 58
Clasmatocolea crassimarginata Grolle 69
Clasmatocolea crassiretis (Herz.) Grolle 124
Clasmatocolea ctenophylla (Schiffn.) Grolle 119
Clasmatocolea cucullistipula (Steph.) Grolle 183
Clasmatocolea cuneifolia (Hook.) Spruce 191
Clasmatocolea doellingeri (Nees) Steph. 191
Clasmatocolea exigua Steph. 192
Clasmatocolea fasciculata (Nees) Grolle 91
Clasmatocolea fiordlandiae (Hodgs.) Grolle 192
Clasmatocolea flavovirens (Steph.) Herz. 99
Clasmatocolea fragillima Spruce 192
Clasmatocolea fulvella (Hook. f. & Tayl.) Grolle 139
Clasmatocolea gayana (Mont.) Grolle 112
Clasmatocolea georgiensis (Gott.) Grolle 193
Clasmatocolea heterostipa Spruce 40, 97
Clasmatocolea humilis (Hook. f. & Tayl.) Grolle 74
Clasmatocolea humilis (Hook. f. & Tayl.) Grolle var. humilis 80
Clasmatocolea humilis var. polymorpha Engel 91
Clasmatocolea humilis var. suspecta (Mass.) Engel 88
Clasmatocolea innovata Herz. 193
Clasmatocolea koeppensis (Gott.) Grolle 44
Clasmatocolea marginata (Steph.) Grolle 69
Clasmatocolea minutiretis Engel & Grolle 133
Clasmatocolea moniliformis Engel 128
Clasmatocolea navicularis (Steph.) Grolle 193
Clasmatocolea navistipula (Steph.) Grolle 165
Clasmatocolea navistipula (Steph.) Grolle var. navistipula 169
Clasmatocolea navistipula var. parceramosa Engel 172
Clasmatocolea notophylla (Hook. f. & Tayl.) Grolle 173
Clasmatocolea obvoluta (Hook. f. & Tayl.) Grolle 50
Clasmatocolea obvoluta var. cookiana (Mass.) Engel 58
Clasmatocolea obvoluta (Hook. f. & Tayl.) Grolle var. obvoluta 56
Clasmatocolea paucistipula (Rodw.) Grolle 196
Clasmatocolea planifolia Steph. 196
Clasmatocolea puccioana (De Not.) Grolle 157
Clasmatocolea rigens (Hook. f. & Tayl.) Engel 44
Clasmatocolea rotata (Hook. f. & Tayl.) Grolle 196
Clasmatocolea strongylophylla (Hook. f. & Tayl.) Grolle 147
Clasmatocolea tjiwideiensis (Sande-Lac.) Grolle 154
Clasmatocolea trachyopa (Hook. f. & Tayl.) Grolle 60
Clasmatocolea truncata Steph. 197
Clasmatocolea turgescens (Hook. f. & Tayl.) Grolle 149
Clasmatocolea typhacella Steph. 197
Clasmatocolea vermicularis (Lehm.) Grolle 96
Clasmatocolea verrucosa Engel 179
Clasmatocolea zotovii (Herz.) Grolle 197
Coleochila cuneifolia (Hook.) Dum. 191
Conoscyphus flaccidus Pears. 112
Conoscyphus tjiwideiensis (Sande-Lac.) Schiffn. 154
Cylindrocolea acutiloba (Schiffn.) Engel 191
Cylindrocolea novae-caledoniae (Grolle) Schust. 196

Cylindrocolea rhizantha (Mont.) Schust. 192

Drepanolejeunea stephaniana Mass. 193

Evansianthus georgiensis (Gott.) Schust. & Engel 193

Hepatostolonophora abnormis (Besch. & Mass.) Engel & Schust. 190
Hepatostolonophora paucistipula (Rodw.) Engel 196
Hepatostolonophora rotata var. perssonii (Schust.) Engel 192
Hepatostolonophora rotata (Hook. f. & Tayl.) Engel 196
Heteroscyphus fasciculatus (Nees) Schiffn. 91
Heteroscyphus rabenhorstii (Steph.) Schiffn. 91

Isotachis capensis Steph. *ex* Herz. 93

Jamesoniella difficilis Steph. 171
Jamesoniella gracilis Gola 191
Jungermannia bergiana Lehm. 91
Jungermannia chamissonis Gott. & Lindenb. 97
Jungermannia chilensis Lehm. 193
Jungermannia chilensis Mont. 193
Jungermannia cuneifolia Hook. 191
Jungermannia doellingeri Nees 191
Jungermannia dregeana Lehm. & Lindenb. 91
Jungermannia fasciculata (Lindenb.) Hook. f. & Tayl. 91
Jungermannia fasciculata Nees 91
Jungermannia flexuosa Lehm. 97
Jungermannia fulvella Hook. f. & Tayl. 139
Jungermannia gayana Mont. 112
Jungermannia humilis Hook. f. & Tayl. 80
Jungermannia humilis Kash. & Chopra 80
Jungermannia marginata Hook. f. & Tayl. 69
Jungermannia marginata Lehm. 69
Jungermannia marginata Mitt. 69
Jungermannia moniliformis Ångstr. 190
Jungermannia notophylla Hook. f. & Tayl. 173
Jungermannia obvoluta Hook. f. & Tayl. 56
Jungermannia obvolutaeformis De Not. 56
Jungermannia palustris Hook. f. & Tayl. 80
Jungermannia ?puccioana De Not. 157
Jungermannia rigens Hook. f. & Tayl. 44
Jungermannia rotata Hook. f. & Tayl. 196
Jungermannia strongylophylla Hook. f. & Tayl. 147
Jungermannia strongylophylla var. *β minor* Hook. f. & Tayl. 149
Jungermannia subintegra Hook. f. & Tayl. 97
Jungermannia trachyopa Hook. f. & Tayl. 60
Jungermannia turgescens Hook. f. & Tayl. 149
Jungermannia variabilis (Sim) S. Arnell 101
Jungermannia vermicularis Hüb. 96
Jungermannia vermicularis Lehm. 96

Leioscyphus (?) *abnormis* Besch. & Mass. 190
Leioscyphus chamissonis (Gott. & Lindenb.) Spruce 97
Leioscyphus cuneifolius (Hook.) Steph. 191
Leioscyphus humilis (Hook. f. & Tayl.) Pears. 80
Leioscyphus marginatus Steph. 69
Leioscyphus patagonicus Pears. 88
Leioscyphus patagonicus Steph. 88
Leioscyphus strongylophyllus (Hook. f. & Tayl.) Mitt. 147
Leioscyphus turgescens (Hook. f. & Tayl.) Mitt. 149
Lejeunea subintegra (Hook. f. & Tayl.) G. L. & N. 97
Leptoscyphus chamissonis (Gott. & Lindenb.) Mitt. 97
Leptoscyphus cuneifolius (Hook.) Mitt. 191

Leptoscyphus liebmanianus (Lindenb. & Gott.) Mitt. 192
Leptoscyphus porphyrius (Nees) Grolle 193
Leptoscyphus strongylophyllus (Hook. f. & Tayl.) Mitt. 147
Leptoscyphus turgescens (Hook. f. & Tayl.) Mitt. 149
Lophocolea abnormis (Besch. & Mass.) Steph. 190
Lophocolea angulistipula Steph. 149
Lophocolea arenaria Schiffn. 60
Lophocolea austrigena (Hook. f. & Tayl.) G. L. & N. 24, 82, 177
Lophocolea boliviensis S. Arnell 99
Lophocolea boliviensis Steph. 99
Lophocolea boveana Mass. 24
Lophocolea catenulata Herz. 81
Lophocolea concava Steph. 117
Lophocolea cookiana Mass. 58
Lophocolea crassiretis Herz. 124
Lophocolea cristato-spinosa Steph. 119
Lophocolea ctenophylla Schiffn. 119
Lophocolea cucullifolia Steph. 186
Lophocolea cucullistipula Steph. 183
Lophocolea debilis Steph. 44
Lophocolea diversistipa Steph. 159
Lophocolea elata f. *aquatica* Herz. 101
Lophocolea fasciculata (Nees) S. Arnell & Grolle 91
Lophocolea filiformis Steph. 186
Lophocolea fiordlandiae Hodgs. 192
Lophocolea flavovirens Steph. 99
Lophocolea fulvella (Hook. f. & Tayl.) Mass. 139
Lophocolea gayana (Mont.) Mitt. 112
Lophocolea georgiensis Gott. 193
Lophocolea gottscheoides Besch. & Mass. 24
Lophocolea gunniana Nees 24, 82, 177
Lophocolea hickenii Herz. 88
Lophocolea hastatistipa Steph. 80
Lophocolea homomalla Steph. 139
Lophocolea humilis (Hook. f. & Tayl.) Steph. 80
Lophocolea incrassata Steph. 80
Lophocolea integerrima Steph. 80
Lophocolea koeppensis Gott. 44
Lophocolea lacerata Steph. 60
Lophocolea latissima Steph. 58
Lophocolea lenta (Hook. f. & Tayl.) G. L. & N. 21, 24, 48
Lophocolea leptantha (Hook. f. & Tayl.) G. L. & N. 24
Lophocolea ligulata Steph. 99
Lophocolea longissima Steph. 99
Lophocolea magellanica Schiffn. 80
Lophocolea minima S. Arnell 101
Lophocolea multispinula Steph. 88
Lophocolea navicularis Steph. 193
Lophocolea navistipula Steph. 169
Lophocolea notophylla (Hook. f. & Tayl.) Hodgs. 173
Lophocolea obvoluta (Hook. f. & Tayl.) Evans 56
Lophocolea obvolutaeformis (De Not.) Mass. 56
Lophocolea okaritana Steph. 177
Lophocolea olens Herz. 44
Lophocolea otiphylla (Hook. f. & Tayl.) Mitt. 24, 82
Lophocolea ovistipula Herz. 101
Lophocolea palustris (Hook. f. & Tayl.) Besch. & Mass. 80
Lophocolea patagonica Beauv. 159
Lophocolea paucistipula Rodw. 196
Lophocolea puccioana (De Not.) Mass. 157
Lophocolea puccioana a* forma *primigenia* Mass. 157
Lophocolea puccioana var. *β primigenia* (Mass.) Schiffn. 157
Lophocolea puccioana var. *β suspecta* Mass. 88
Lophocolea rigens (Hook. f. & Tayl.) Evans 44
Lophocolea rotundifolia Steph. 81
Lophocolea rotundistipula Steph. (1906) 159
Lophocolea rotundistipula Steph. (1911) 159
Lophocolea sabuletorum (Hook. f. & Tayl.) G. L. & N. 24, 103
Lophocolea skottsbergii Steph. 99
Lophocolea stephanii Herz. 44
Lophocolea stephanii Schiffn. 44
Lophocolea strongylophylla (Hook. f. & Tayl.) Hodgs. 149
Lophocolea subaromatica Herz. 49
Lophocolea subcapillaris Steph. 171

Lophocolea subintegra (Hook. f. & Tayl.) Grolle 97
Lophocolea subulistipa Herz. 101
Lophocolea tesorensis Herz. 110
Lophocolea textilis (Hook. f. & Tayl.) G. L. & N. 24
Lophocolea trachyopa (Hook. f. & Tayl.) G. L. & N. 60
Lophocolea tumida Steph. 173
Lophocolea turbiniflora Steph. 99
Lophocolea turgescens (Hook. f. & Tayl.) Hodgs. 149
Lophocolea vermicularis Herz. 93
Lophocolea vinciguerreana Mass. 112
Lophocolea zotovii Herz. 197

Mesophylla strongylophylla (Hook. f. & Tayl.) Trev. 147
Microlejeunea chilensis (Mont.) Steph. 193
Mylia chamissonis (Gott. & Lindenb.) Trev. 97
Mylia humilis (Hook. f. & Tayl.) Trev. 80
Mylia turgescens (Hook. f. & Tayl.) Trev. 149
Mylius cuneifolius (Hook.) S. Gray 191
Myriocoleopsis puiggari Schiffn. 197

Nardia humilis (Hook. f. & Tayl.) Berggr. 80
Nardia lindmanii Steph. 97
Nardia vermicularis (Lehm.) Trev. 96
Notoscyphus belangerianus (Lehm.) Mitt. 104
Notoscyphus flexuosus (Lehm.) Sim 97
Notoscyphus lindmanii (Steph.) Schiffn. 97
Notoscyphus variifolius Mitt. 97
Notoscyphus vermicularis (Lehm.) Steph. 96

Odontoschisma marginatum (Steph.) Steph. 69
Odontoschisma variabile (Lindenb. & Gott.) Trev. 101
Odontoschisma variabile Sim 101

Pedinophyllum interruptum subsp. truncatum (Steph.) Inoue 197
Phragmatocolea innovata (Herz.) Grolle 193

Solenostoma humilis (Hook. f. & Tayl.) Mitt. 80
Solenostoma rotatum (Hook. f. & Tayl.) Mitt. (1867) 196
Solenostoma rotatum (Hook. f. & Tayl.) Mitt. *ex* Bastow (1888) 196
Stolonophora abnormis (Besch. & Mass.) Engel & Schust. 190

Xenocephalozia navicularis (Steph.) Schust. 193

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